

Natural selection for rare and mimetic colour pattern combinations in wild populations of the diadem butterfly, *Hypolimnas misippus* L.

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Mark recapture and morph frequency data, gathered during a population irruption of *Hypolimnas misippus* in southern Ghana, provide evidence for apostatic and mimetic selection. During a period of low adult survival, both the recapture rate and the frequency of the commonest morph (*misippus*) were significantly reduced. Selection against this form increased phenotypic diversity and generated significant disequilibrium in the combinations of unlinked fore- and hindwing phenotypes. There was also evidence for selection against those forms (weak *alcippoides*) which most closely resemble *misippus*. Other morphs, including both good mimics of *Danaus chrysippus* and rare non-mimics, showed no reductions in recapture rate during the period of low survival, but only the good mimics increased significantly in frequency. The results provide a predictive ecological model for density-dependent selection by predators which is consistent with field data from previous studies of *H. misippus* in Ghana and Tanzania. Their evolutionary implications are discussed, and it is suggested that anomalies in the mimicry of this species may be partly due to lack of predation when it is scarce.

KEY WORDS:—*Hypolimnas misippus* – *Danaus chrysippus* – Batesian mimicry – density-dependent selection – mimetic selection – apostatic selection – epistatic selection – linkage disequilibrium.

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INTRODUCTION

Bates (1862) suggested that convergent resemblances between unrelated butterflies evolved because of selection by predators. In particular he argued that palatable species would gain protection from predators by resembling unpalatable species, a situation now known as Batesian mimicry. This theory is widely accepted and has been extended and modified to cover a variety of situations and organisms. It is therefore surprising that there are few accounts of mimicry in action in natural populations. As recently as 1979, Jeffords, Sternburg & Waldbauer could claim priority in demonstrating the efficacy of Batesian mimicry in the field. In this and earlier studies (Brower, Stiles, Croze & Homer, 1964; Brower, Cook & Croze, 1967; Cook, Brower & Alcock, 1969; Benson, 1972; Sternburg, Waldbauer & Jeffords, 1977) artificial mimics and non-mimics were created by painting insect wings. In no case has selection for mimicry been detected and analysed in a natural population of polymorphic mimics.

A similar situation exists with regard to the more recent theory of apostatic selection (frequency-dependent predation on common forms of polymorphic prey) (Clarke, 1962), in that studies demonstrating its occurrence in natural populations are also scarce. Clarke (1979) states that "its widespread occurrence has been established beyond doubt", yet most of the work with which he justifies this claim has been experimental, involving predators in the laboratory or artificial baits in the field. Strictly speaking, what has been established beyond doubt is the widespread capacity of predators for apostatic selection rather than its widespread occurrence. According to Allen (1984), "the following words still stand: 'the most important point now is whether sight-dependent predators can be trained to search for a particular morph of a natural polymorphic species' (Allen, 1974, p. 370)". Even if this point is established by appropriate experiments, studies of predator interactions with polymorphic prey in natural conditions will be necessary to determine just how common apostatic selection really is, and to examine how it interacts with other forms of predator selection (e.g. for mimicry).

In this paper, I present evidence for density-dependent apostatic and mimetic selection during a population irruption of the diadem butterfly, *Hypolimnas misippus* in southern Ghana. Mark-recapture data show significant changes in survival rates and frequencies of rare and common mimics and non-mimics. The patterns of these changes support the interpretation that this species is a Batesian mimic of the African queen butterfly, *Danaus chrysippus* L., and suggest an ecological model for intermittent selection by predators that is testable against field data. Results from earlier studies of *H. misippus* in Ghana (Edmunds, 1969) and Tanzania (Smith, 1976) support the model. I end by considering some of the evolutionary implications of the new findings.

MODELS AND MIMICS

Named colour pattern morphs of the diadem and the queen are shown in Fig. 1. There are four matching pairs of mimics and models: *misippus/aegyptius*; *alcippoides/alcippus*; *inaria/dorippus*; *inaria-alcippoides/albinus*. In *H. misippus*, there is a phenotypic continuum between the mimetic extremes shown in Fig. 1, and non-mimetic intermediates may be common (Edmunds, 1969; Smith, 1976). In



Figure 1. Polymorphic mimicry in *Hypolimnas misippus* and *Danaus chrysippus*. On the left, from top to bottom, the four named forms of *Hypolimnas misippus*: *misippus*, *alcippus*, *inaria*, and *inaria-alcippoides*. On the right, from top to bottom, the four forms of *Danaus chrysippus*: *aegyptius*, *alcippus*, *dorippus* and *albinus*. All four forms of *H. misippus*, but only the *alcippus* form of *D. chrysippus*, are found in Ghana. Stippled areas are orange.

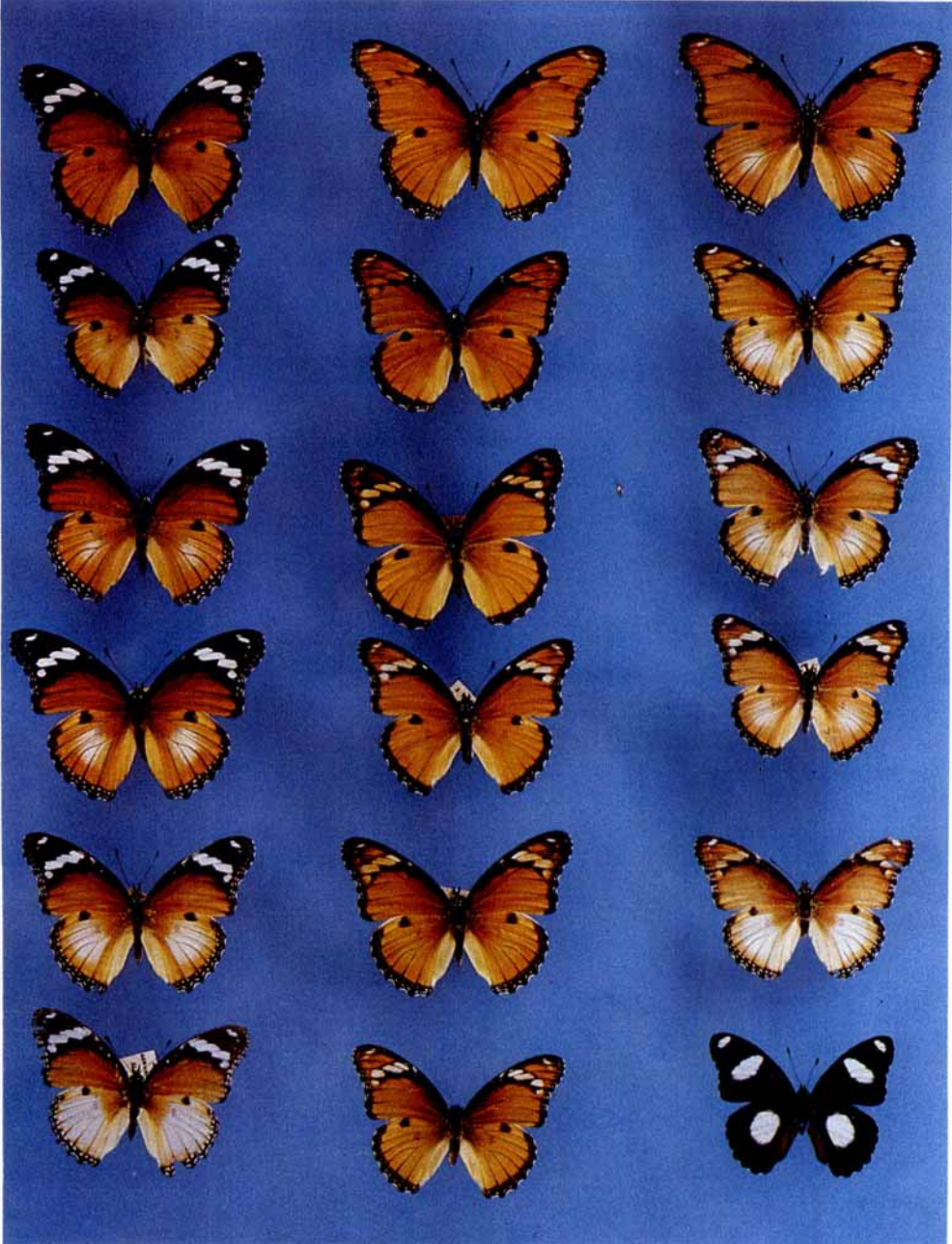


Figure 2. Range of colour patterns in *Hypolimnas misippus*. On the left, from top to bottom: *misippus* (blw 0), weak *alcippoides* (blw 2, blw 3), strong *alcippoides* (blw 4, blw 5, blw 8). Centre, from top to bottom: *inaria* (oo 0, bro 0, brp 0, ow 0, brp 0, ow 0). On the right, from top to bottom *inaria-alcippoides* (oo 3, op 4, brw 4, ow 4, op 8), and a male diadem.

D. chrysippus, there may be minor expression of recessive phenotypes in heterozygotes, but there is no continuum between forms and obvious intermediates are rare (Smith, 1980). *Hypolimnas misippus* is always polymorphic in Africa but *D. chrysippus* is often monomorphic. Male colour patterns in

H. misippus are male-limited, non-mimetic and probably ancestral; in *D. chrysippus* males and females share identical colour patterns. Figure 2 shows several of the intermediate colour patterns found in female diadems together with that of the male.

Mimicry seems to be Batesian rather than Mullerian for several reasons. First, it is female-limited in *H. misippus*. Second, the colour patterns of female diadems are polymorphic and highly variable (Fig. 2), with both mimetic and non-mimetic forms (Edmunds, 1969; Smith, 1976). The African queen, although polymorphic in eastern and central Africa, is monomorphic in western, northern and southern Africa (Owen, 1971; Pierre, 1973). Third, *H. misippus* is not known to be distasteful whereas *D. chrysippus* sequesters and stores Class 1 defensive compounds (Brower, 1984; Boppré, 1984). Fourth, *D. chrysippus* has the life style of a protected and toxic butterfly (Rothschild, von Euw, Reichstein, Smith & Pierre, 1975) while that of *H. misippus* is characteristic of a "true Batesian mimic" (Marshall, 1902).

Despite these facts and the impressive resemblances shown in Fig. 1, there is no agreement as to the mimetic status of *Hypolimnas misippus*. Poulton (1908) believed it to be a Mullerian mimic, a suggestion recently revived by Marsh, Clarke, Rothschild & Kellett, (1977). Bernardi (1963, 1974) and Pierre (1973, 1980) question whether the relationship is mimetic at all. These disagreements arise because of widespread mismatching in the geographical ranges of corresponding forms in the two species (Bernardi, 1963, 1974; Pierre, 1973, 1980). Mimics are found thousands of miles away from their supposed models. Even where all four pairs of morphs occur together, they fail to correspond in frequency rank (Smith, 1976). Other anomalies include the following: (i) aposematic colour patterns in the mimic do not break down in the absence of their models (Pierre, 1973); (ii) non-mimetic intermediates are more common in Tanzania where all forms of the model are found than in Ghana where only one form exists (Edmunds, 1969; Smith, 1976); (iii) clinal variation in the forewing pattern of *D. chrysippus* is not followed by its mimic (Pierre, 1973); and (iv) the mimic is sometimes much more abundant than its model (Poulton, 1908; Edmunds, 1969; Pierre, 1973; Unamba, unpubl. data). These observations are hard to reconcile with the expectations of Batesian mimicry.

METHODS

Hypolimnas misippus is an irruptive butterfly which becomes suddenly abundant following the early rains of the major and minor rainy seasons. Sampling was therefore started immediately after the first rains at the end of the dry season (on 4 March 1977, after 13 mm of rain on the 3 March) and continued until the beginning of August when the major rains were over. It was conducted on a daily basis in the Botanical Gardens of the University of Cape Coast campus. The sampling period lasted for 2 h each day, generally between 10 and 12 in the morning when females are most active (Edmunds, 1969). Occasional samples were missed or shortened due to continuous rain or other commitments. New butterflies were given individual marks with 'Magic Marker' pens, and the marks of recaptures were recorded without further marking. Individual marking was possible by using different combinations of colours and positions on left and right hindwings. Butterflies were released at the

point of capture after recording their sex and morph. The latter was only necessary in the females as males are non-mimetic and monomorphic. Data on the males are ignored in the present paper. Population and survival estimates were calculated by the Fisher–Ford and Jolly mark–recapture methods using the MARKREC program at the University of Manchester.

Colour pattern was recorded using the system of Edmunds (1969). The colour of the forewing apex was recorded as black (bl), brown (br) or orange (o), and that of the sub-apical band as white (w), pale orange (p) or orange (o). The quantity of white in the hindwing was recorded by the number of internervular spaces containing white scales: this figure varied between zero and 8. Thus, using this system, the *Hypolimnas* butterflies in Figure 1 would be recorded as blw 0 (*missippus*), blw 8 (*alcippoides*), oo 0 (*inaria*) and oo 8 (*inaria-alcippoides*). Intermediate forms were recorded as shown in Fig. 2.

For the purposes of analysis, the following five morph classes were distinguished: *missippus*, blw 0; weak *alcippoides*, blw 1–3; strong *alcippoides*, blw 4–8; *inaria*, oo 0, op 0, ow 0, bro 0, brp 0, brw 0; and *inaria-alcippoides*, oo 1–8, op 1–8, ow 1–8, bro 1–8, brp 1–8, and brw 1–8. Examples are illustrated in Fig. 2. To avoid confusion, latin names for the various morphs will only be italicized when they refer specifically to the phenotype combinations listed above. Italics will not be used when referring separately to fore- or hindwing phenotypes: *inaria* will thus refer to the oo–brw forewing patterns, *missippus* to the blw forewing pattern, and *alcippoides* to white (1–8) hindwings. The justification for this classification is both genetic and phenotypic. All the *inaria* forms are genotypically *mm* at the main forewing locus, while the *missippus* forms are *M*– (Smith & Gordon, in prep.). The strong and weak forms of *alcippoides* are distinguished on the grounds that the former are good mimics of *D. chrysippus* in Ghana and are quite distinct from the common *missippus* morph, while the latter are weak mimics and resemble *missippus*. Only the *alcippus* form of *D. chrysippus* occurs in Ghana, so that only the *alcippoides* forms of *H. missippus* are mimetic.

It was not possible to simultaneously sample both models and mimics without adverse effects on the sample sizes of the latter. However, a limited number of morning and afternoon samples of *D. chrysippus* were obtained in March, and records of sightings during *Hypolimnas* sampling were kept until the last week of April.

RESULTS

Population changes

Figure 3 shows (for the polymorphic females alone) changes in capture rate and in Fisher–Ford and Jolly population estimates during the sampling period. Comparison of the three sets of data reveals consistent tracking of population change and reasonable agreement between the two population estimates until the end of the major irruption. There then followed a period (7–31 May) during which the Fisher–Ford estimates clearly fail to track population change (as revealed by the raw capture rate data) and were considerably larger than the Jolly estimates. The latter tracked the capture rate data with reasonable accuracy, so that the Fisher–Ford method appeared to be overestimating population size during this period. Subsequently in June and July, the

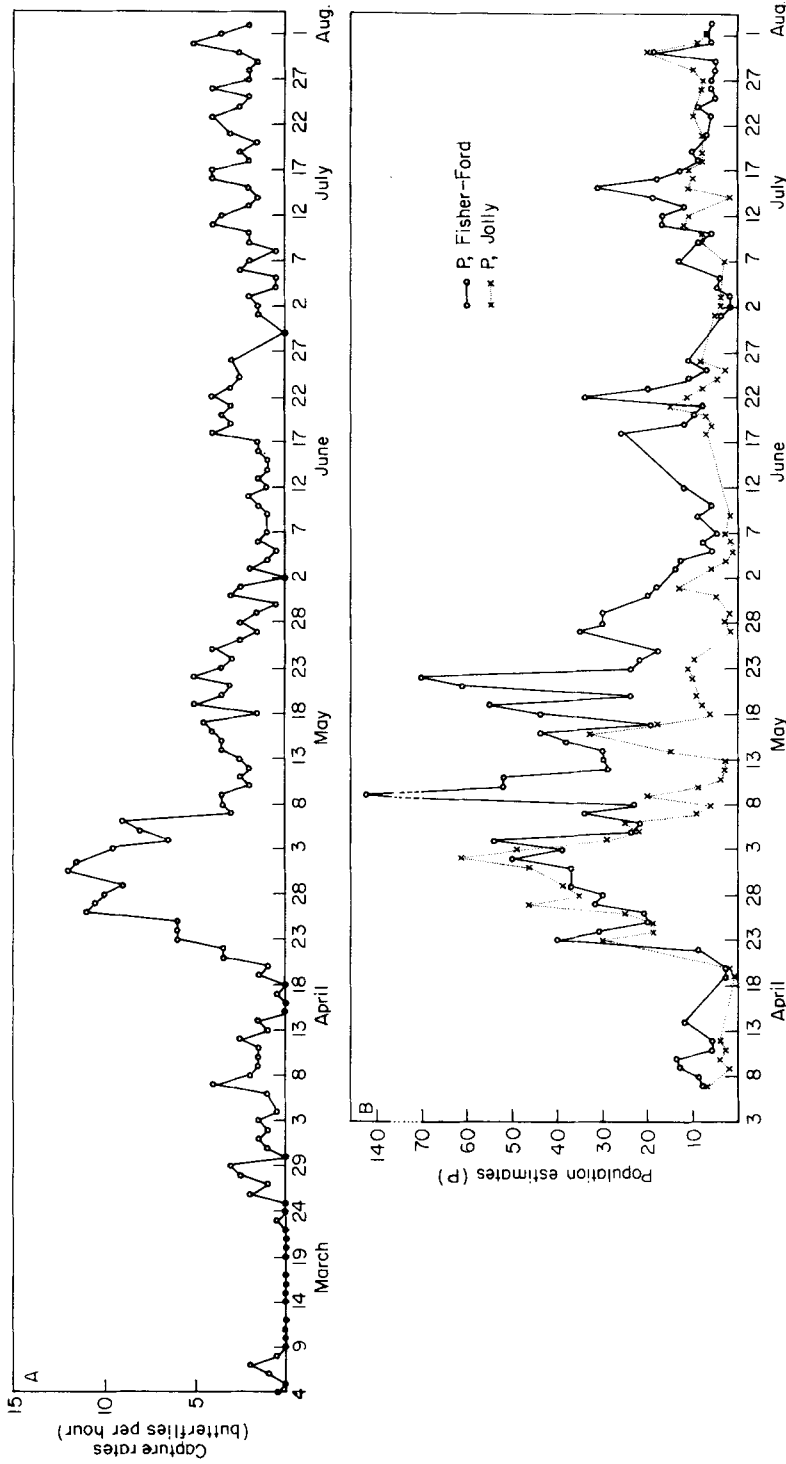


Figure 3. A, Capture rates and B, Fisher-Ford and Jolly population estimates during an irruption of *Hypolimnas misippus* at Cape Coast (March-August, 1977).

Fisher–Ford estimates recovered their earlier consistency. Although discrepancies occurred in this period, they were minor compared with those in May.

Survival rates

The Fisher–Ford method assumes a constant survival rate and calculates this by iteration. For the entire sampling period this was 74.3% per day with 95% confidence limits between 72.5 and 76.2%. The Jolly method provides daily estimates (data permitting) which may be very different. Their geometric mean for the entire period was 61.7%.

The validity of the Fisher–Ford assumption of a constant survival rate may be tested by comparing the observed and expected numbers of days survived (Begon, 1979). the difference between them is highly significant ($\chi^2_{(87)} = 334.0$, $P < 10^{-10}$). Variation in real survival rate means that the Fisher–Ford method overestimates population size when survival rates are lower than average. This appears to have been the case from 7 to 31 May: the geometric mean of the Jolly survival rate estimate for this period was 43.4%, as compared to 68.1% for the period before and 70.1% in June and July.

Figure 4 shows changes in survival rates calculated as five day running geometric means of the daily Jolly estimates (ignoring days for which no estimates are available). These running means were lower than the overall mean from 5 May to 7 June. Their brief recovery between 13 and 17 May coincides with a short-lived improvement in the agreement between Fisher–Ford and Jolly population estimates. The serial correlation imposed by the calculation of running means makes the exact timing of changes in survival rate uncertain, but there can be little doubt that there was a real drop in survival in May and that this was responsible for the discrepancies in population estimates at this time.

Recapture rates

Table 1 presents the recapture rates of the different morphs (with *inaria* and *inaria-alcippoides* combined for reasons of sample size) for the three periods recognised above. Only the commonest morph (*misippus*), and the forms which most closely resemble *misippus* (weak *alcippoides*) were recaptured less frequently in the middle period of low survival, the former significantly so and the latter not. The rarer forms which do not resemble *misippus* were clearly unaffected:

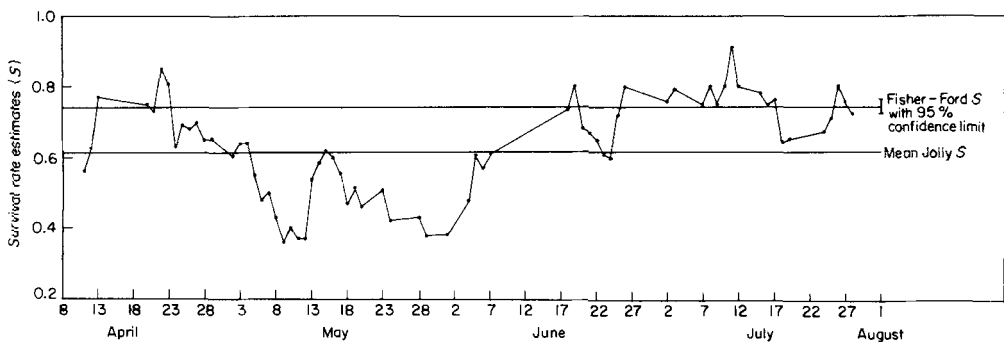


Figure 4. Geometric running means of the daily Jolly survival rates.

Table 1. Recapture rates of different morphs before, during and after the period of low survival

Morph	Period						$\chi^2_{(2)}$
	4/3-6/5		7/5-31/5		1/6-2/8		
	%R	N	%R	N	%R	N	
<i>misippus</i>	43.2	74	15.6	32	33.9	56	7.55*
weak <i>alcippoides</i>	33.3	33	16.7	18	39.4	33	2.79
strong <i>alcippoides</i>	33.3	18	37.5	24	31.3	16	0.18
<i>inaria</i> and <i>inaria-alcippoides</i>	32.5	40	40.0	25	25.0	20	1.14

%R is the percentage of new butterflies that were recaptured. N is the sample size. *Inaria* and *inaria-alcippoides* are combined to increase sample size. Samples for the second and third period include new butterflies that were captured the day before the period began; such butterflies are therefore excluded from the respective preceding periods.

* $P < 0.025$.

neither good mimics of *D. chrysippus* (strong *alcippoides*) nor non-mimics (the *inaria* forms) showed any reduction in May recapture rates. Collectively they had a significantly higher recapture rate (38.7%) between 7 and 31 May than the combined class of *misippus* and weak *alcippoides* (16.0%) ($\chi^2 = 5.37$, $P < 0.05$). These figures suggest that the latter suffered a selective disadvantage of some 59% relative to the other forms.

Morph frequencies

Morph frequency data are presented in Table 2 for the same periods considered in Table 1. They are based on samples of new butterflies only and are therefore independent of the recapture rate data. Overall changes (Table 2a) were significant ($\chi^2_{(2)} = 16.92$, $P < 0.05$). There were significant differences between the first and second ($\chi^2_{(4)} = 10.47$, $P < 0.05$) and between the second and third periods ($\chi^2_{(4)} = 10.95$, $P < 0.05$), but not between the first and the third. The χ^2 values in the table test each morph separately and were only significant for *misippus* and strong *alcippoides*. The former fell from 45.3 to 30.2% in the period of low survival, recovering to 45.1% in the third period. The latter rose from 11.6 to 25.0%, dropping to 12.3% in the last period. The other forms, including both weak mimics and rare non-mimics, showed no significant changes in frequency.

Table 2b shows the percentages of white hindwings in butterflies with *misippus* and *inaria* forewings for the three periods considered above. The data demonstrate significant linkage disequilibrium confined to the middle period of low survival. During this period there were significantly more white hindwings combined with *misippus* forewings than with *inaria* forewings.

Table 2c shows estimates of phenotypic diversity, calculated (following Smith, 1976) as the reciprocal of Simpson's diversity index. This has a maximum value of 5 (corresponding to the number of phenotype classes recognized here) and a minimum value of 1. It peaked during the middle period at 4.51.

The figures in Table 2 were calculated for sampling intervals which were

Table 2. Morph frequencies, phenotype combinations, and phenotypic diversities before, during and after the period of low survival

	Period			$\chi^2_{(2)}$		
	4/3-6/5	7/5-31/5	1/6-2/8			
(a) Morph frequencies						
	%	%	%			
<i>misippus</i>	45.3	30.2	45.1	6.73*		
weak <i>alcippoides</i>	19.2	19.8	26.2	2.33		
strong <i>alcippoides</i>	11.6	25.0	12.3	9.65**		
<i>inaria</i>	15.7	17.7	12.3	1.30		
<i>inaria-alcippoides</i>	8.1	7.3	4.1	1.95		
<i>N</i>	172	96	122			
(b) Phenotype combinations						
	% <i>A</i>	<i>N</i>	% <i>A</i>	<i>N</i>	% <i>A</i>	<i>N</i>
<i>misippus</i>	40.5	131	59.7	72	46.1	102
<i>inaria</i>	34.1	41	41.2	24	25.0	20
χ^2	0.29		5.57**		2.24	
(c) Phenotypic diversities						
	$1/\lambda$	$1/\lambda$	$1/\lambda$			
	3.53	4.51	3.35			

N is sample size. %*A* is percent *alcippoides* in butterflies with *misippus* and *inaria* forewings. λ is Simpsons diversity index (see text). Frequency changes in Table 2a are tested separately for each morph.

* $P < 0.05$. ** $P < 0.02$.

independently defined by reference to changes in survival rate. This means that periods of unequal length are compared and information on possible changes during the longer periods is lost. Morph frequencies were therefore also calculated for successive intervals of 32, 30, 30, 30 and 29 days, chosen such that the middle period began on 5 May when the survival rate started to decline (Fig. 4). A 30-day interval (when possible) is appropriate since this is approximately equal to the generation time at Cape Coast.

The results are shown in Fig. 5 and Table 3. Figure 5 illustrates just how unusual the morph frequencies were in May and early June. The percentage of good mimics at this time rose to 26.8% while that of *misippus* fell to 30.4%. The morph frequencies for May/June differed significantly from both the preceding ($\chi^2_{(4)} = 12.31$, $P < 0.02$) and the following period ($\chi^2_{(4)} = 9.85$, $P < 0.05$). The latter change resulted from rapid restoration of more normal morph frequencies: those for the fourth period were not significantly different from those for the second. There were no significant changes between the first and the second or the fourth and the fifth periods. The data on phenotype combinations shown in Table 3a show the same pattern: significant disequilibrium was confined to the May/June sample. Phenotypic diversity also peaked at this time (Table 3b).

Figure 6 compares the distribution of white in the hindwings of *alcippoides* (blw 1-8) during 5 May to 3 June with that for other periods. There were

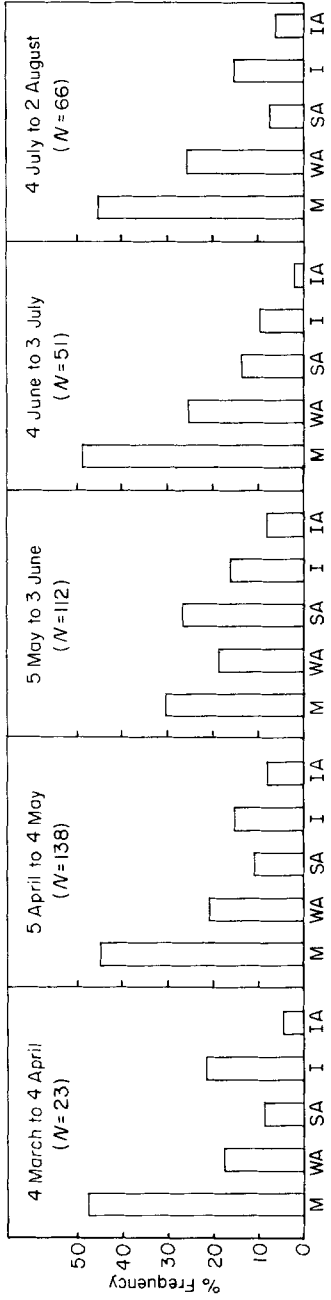


Figure 5. Morph frequencies during successive 30-day periods. KEY: M, *missippus*; WA, weak *alcippoides*; SA, strong *alcippoides*; I, *inaria*; IA *inaria-alcippoides*.

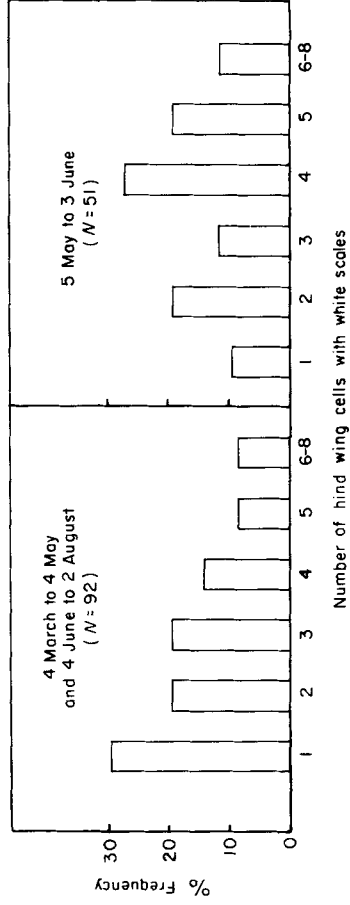


Figure 6. Distribution of hindwing white in samples of *alcippoides*.

Table 3. Phenotype combinations and phenotypic diversities for successive 30-day periods

	Period									
	4/3-4/4		5/4-4/5		5/5-3/6		4/6-3/7		4/7-2/8	
(a) Phenotype combinations	%A	N	%A	N	%A	N	%A	N	%A	N
<i>misippus</i>	35.3	17	41.5	106	60.0	85	44.4	45	42.3	52
<i>inaria</i>	16.7	6	34.4	32	33.3	27	16.7	6	28.6	14
	P = 0.38		$\chi^2 = 0.27$		$\chi^2 = 4.84^*$		P = 0.20		$\chi^2 = 0.39$	
(b) Phenotypic diversities	1/ λ		1/ λ		1/ λ		1/ λ		1/ λ	
	3.51		3.54		4.46		3.12		3.39	

%A, N and λ as in Table 2. Fisher's exact probability test is applied in Table 3a when sample sizes are too small for the χ^2 test.

* $P < 0.05$.

significant differences in the overall distribution of white ($\chi^2_{(5)} = 13.29$, $P < 0.025$) as a result of a shift towards more white in the May/June sample. Only 41.2% were weak *alcippoides* (blw 1-3) as compared to 58.8% for the other periods ($\chi^2 = 9.00$, $P < 0.01$). Only 9.8% were blw 1 in May/June, compared with 29.3% for other periods ($\chi^2 = 6.13$, $P < 0.02$).

Model abundance

Table 4 shows capture rates for *D. chrysippus* in the Botanical Gardens during sampling in March, together with records of the numbers of sightings during *Hypolimnas* sampling in March and April. After 25 April, no further records of model abundance were kept other than a note on 27 May that *Danaus* was becoming scarce. Grass cutting and mowing temporarily affected numbers by destroying flowers of *Tridax procumbens* (e.g. in the last week of March). The presence of large stands of this important adult foodplant made the Botanical Gardens a particularly attractive habitat for *D. chrysippus*.

Predators

Only one act of predation was witnessed during the sampling period: an old and worn butterfly was caught in a spider's web and killed. No vertebrates were observed attacking butterflies between March and August, although on two other occasions rainbow lizards were seen to capture and eat female *Hypolimnas*. Table 5 lists potential vertebrate predators. The bird list (plus comments on status and migration dates) is extracted from the records of Dr M. A. Macdonald, made within a 15 km radius of Cape Coast from 1975 to 1978. The most interesting fact in the table is the last sighting for bee-eaters (6 June) (Macdonald, 1979), a date which coincides with the end of the period of low survival in Figure 4.

Table 4. Capture rates (March) and sightings (March–April) of *Danaus chrysippus* in the Botanical Gardens

Date (March)	Numbers		Date (April)	Numbers seen
	Seen	Caught		
4	98	—	1	37
5	160	—	2	59
6	133	—	3	46
7	105	31	4	91
8	80	29	6	88
9	49	22	7	92
10	86	—	8	103
11	89	—	9	82
12	123	—	10	86
14	94	35	11	56
15	113	32	12	68
16	81	25	13	138
21	83	35	14	96
22	77	20	15	135
23	64	32	16	114
24	110	—	17	154
25	57	—	18	152
26	76	—	19	143
27	61	—	20	140
28	50	18	21	158
29	70	18	22	136
30	58	11	23	105
31	43	—	24	109
			25	94
Means	85.7	25.7		103.4

Capture rate figures are for new butterflies which were caught between 09.30–10.30, except during 28–30 March when sampling was from 15.30–16.30. Sightings were obtained during the routine two hour *Hypolimnas* samples.

DISCUSSION

Interpretation of the data

The following results require explanation: (i) Fisher–Ford population estimates were excessive in May; (ii) survival rates were low in May; (iii) recapture rates of the commonest morph were significantly reduced in May; (iv) the frequency of the commonest morph was significantly reduced in May; (v) recapture rates of good mimics and rare non-mimics were unaffected in May; (vi) good mimics were the only forms to significantly increase in May; (vii) the distribution of white in *alcippoides* hindwings was shifted towards mimicry and away from the common colour pattern in May; (viii) phenotypic diversity peaked in May; (ix) linkage equilibrium was significantly disturbed in May; and (x) all these changes took place at the same time and were reversed in June. There are synchronous changes in independent sets of data, e.g. (iii) and (iv), indicating common cause and real events.

All the reported results are explained if the common cause was selective predation in May, favouring rare forms and good mimics. Notice that this hypothesis not only explains each fact in isolation, it also explains all of them at once. Four of them deserve further comment.

Table 5. Potential vertebrate predators in the Cape Coast area

Species			
Scientific name	Common name	Status	Present
<i>Agama agama</i>	Rainbow lizard	Abundant	All year
<i>Merops albicollis</i>	White-throated bee-eater	Abundant	Oct.-June Last sighting: 6 June
<i>Eurystomus glaucurus</i>	Broad-billed roller	Common	Nov.-Mar. Last sighting: 24 Mar.
<i>Bubuculus ibis</i>	Cattle egret	Abundant	Main season: Oct.-May
<i>Lanius collaris</i>	Fiscal shrike	Common	All year
<i>Laniarius barbarus</i>	Gonolek	Common	All year
<i>L. aethiopicus</i>	Bellshrike	Common	All year
<i>Tchagra senegala</i>	Black-headed bush-shrike	Common	All year
<i>T. australis</i>	Brown-headed bush-shrike	Common	All year
<i>Dryoscopus gambiensis</i>	Puffback	Common	All year
<i>Pycnonotus barbaratus</i>	Bulbul	Abundant	All year
<i>Terpsiphone rufiventer</i>	Paradise flycatcher	Rare	All year
<i>Dicrurus adsimilis</i>	Drongo	Rare	All year
<i>Halycon senegalensis</i>	Senegal kingfisher	Common	All year
<i>Centropus senegalensis</i>	Senegal coucal	Common	All year

The significant shift in the distribution of hind wing white from less to more during the period of low survival [(vii) above, Fig. 6] is important evidence for the predation hypothesis. A visually hunting predator is unlikely to distinguish between a *misippus* (blw 0) and a weak *alcippoides* with only one white intervein (blw 1). The latter will be included in the search image established for the former.

The observation of significant linkage disequilibrium in May [(ix) above, Tables 2 and 3] requires explanation. Fore- and hindwing phenotypes are determined by genes at unlinked loci (Smith & Gordon, in prep.), so that the percentage of white hindwings will normally be the same in butterflies with inaria forewings as it is in those with misippus forewings. This equilibrium is disturbed if any one combination of fore- and hindwing colour patterns is favoured or selected against. Selection for strong *alcippoides* and against *misippus* thus explains the linkage disequilibrium in May, with equilibrium restored in June through sexual reproduction and random assortment of chromosomes. According to Lewontin (1974), "*The observation of significant linkage disequilibrium that is consistent between populations is a very sensitive detector of natural selection*" (author's italics).

The timing of the period of low survival in relation to that of the irruption [(x) above, Figs 3 and 4] makes sense if predation was density-dependent. Survival rates fell soon after peak numbers of *Hypolimnna* were reached, and improved after numbers had been low for some time. This suggests a lagging Type III functional response (Holling, 1965) by predators to the changes in butterfly abundance. The time lags result since neither learning nor forgetting are instantaneous processes. They are made obvious by the rapidity with which population changes took place. If this interpretation is correct, then at least one member of the African insectivorous fauna is a "Monte Carlo predator" (Turner, 1984). Alternatively, the deterioration and improvement of survival may have been caused by the arrivals and departures of predators which had

already learned to attack female diadems. Bee-eaters are prime suspects since survival rates improved when they left (Fig. 4 and Table 5). Either or both of these explanations could apply.

The absence of differences in the recapture rates of good mimics and rare non-mimics [(v) above, Table 1] raises the possibility that strong *alcippoides* were selected for rarity rather than mimicry. However this form was the only one to significantly increase in frequency as a result of the selection against *misippus*. The failure of the rare non-mimics to also increase at this time suggests that they were at a selective disadvantage to good mimics. There are three reasons for believing that this disadvantage was related to mimicry.

First, a more detailed examination of the morph frequency data suggests that the rare non-mimics were predated in late May. Calculation of 7-day running means (for days on which new butterflies were captured) shows that *inaria* peaked in frequency during the week of the 22–28 May at 32.1% ($N = 28$). At this time it was the most abundant form, having overtaken *misippus* (25.0%) and strong *alcippoides* (21.4%). By the next week it had completely disappeared and was not seen again until 17 June. Thirty-five new butterflies were captured during this interval, and the decline from 32.1% to 0% was significant ($\chi^2 = 10.63$, $P < 0.01$). Meanwhile, the good mimics increased steadily, finally peaking at 35.7% for the period 30 May to 9 June ($N = 14$). The disappearance of *inaria* and the persistence of strong *alcippoides* are explained if predators extended their attention to the former, while continuing to avoid the latter. Note how low recruitment from the previous generation renders adult *inaria* vulnerable to total disappearance once attacked, and how this biases the May recapture rate sample towards the earlier part of the month when their survival was high.

Second, the rare non-mimics are phenotypically more diverse than strong *alcippoides* and resemble *misippus* less (Fig. 2). They were collectively no more abundant when survival was low and should therefore have been favoured more than the good mimics. That this was evidently not the case suggests that the latter were protected by their mimetic resemblance to *D. chrysippus*.

Third, there is evidence (discussed below) that the model was both common enough and unpleasant enough to be avoided by predators vulnerable to the effects of its chemical defences.

Alternative explanations

Alternative explanations of the results are possible, but they require moulding to fit the facts. For example, differential emigration could account for the differences in survival and recapture rates, but unless it was localized its effects on morph frequencies would have been cancelled by differential immigration. If this condition was satisfied, it is then necessary to account for the epistasis and linkage disequilibrium that was observed in May: we have to suppose that orange hindwings increased migration rates in combination with *misippus* forewings, but not in combination with *inaria* forewings. Assuming this also to be true, we are left with the question of why differential emigration was restricted to May. It might have been stimulated by a local and temporary deterioration in habitat, but then it is hard to understand why all morphs were not involved. There are differences between morphs in body size (Gordon,

1982) which may affect powers of flight, but these cannot have been responsible since neither the smallest (*alcippoides*) nor the largest (*inaria*) were recaptured less often in May. This fact alone makes a migration hypothesis unlikely, quite apart from all the special pleading it requires.

A predation hypothesis explains more, predicts more and is more parsimonious. The data are consistent with theories of predator behaviour that are supported by substantial experimental evidence. Moreover, only a predation hypothesis can explain how and why it was that the commonest and most mimetic morphs were most affected: these facts are independently predicted under apostatic and mimetic selection; under any other hypothesis they are reduced to coincidence.

Who were the predators?

Of the species listed in Table 5, the white throated bee-eater is the most likely predator. This bird has been seen to catch and eat *H. misippus* in Ghana (Dr L. Cole in Edmunds, 1969) and the survival rate of female diadems in the Botanical Gardens improved when bee-eaters emigrated. Rainbow lizards are also prime suspects but they might not be selective predators. This is because they may be cued by the settling and ovipositing behaviour of female *Hypolimnas* rather than by colour pattern. They are also less likely to have encountered the models since, as Marshall (1902: 550) observed, *D. chrysippus* seldom settles on the ground.

Of the remaining birds, broad-billed rollers emigrated too early to be involved, puffbacks hunt insects on foliage rather than in flight, and the coucal seems too clumsy to catch active butterflies. Senegal kingfishers and egrets, although common elsewhere, were only occasional visitors to the Botanical Gardens. Bulbuls were common everywhere and do include butterflies in their varied diet (I have seen one take an *Acraea*), but they may be immune to the chemical defences of *Danaus* (Swynnerton, 1942; Stimson & Meyers, 1984). The drongo and the paradise flycatcher are rare birds in the Cape Coast region. They are included in the table because both species have been seen to attack *H. misippus* (Poulton, 1915, 1916) and the drongo is the only west African species that is recorded by Mackworth-Praed & Grant (1970, 1973) as a butterfly predator. Fiscal shrikes and egrets freely hunt prey in the presence of humans, but were never seen to take either *Hypolimnas* or *Danaus*. The other shrikes are cover-loving and skulking birds that would be unlikely to be seen taking prey in the open.

There is no reason why only one species should have been involved, particularly in view of the demonstration by Mason, Arzt & Reidinger (1984) of trans-specific observational learning of food preferences and aversions in grackles and blackbirds. Although I failed to observe any vertebrate predation in over 200 hours of field work, most birds are likely to avoid a conspicuous human chasing butterflies with a large net. This will be particularly true when bird and human converge on the same target.

Was the model nasty?

If mimics are to be protected then models must be nasty. The nasty qualities of *D. chrysippus* are opportunistically acquired, so that natural populations

exhibit a palatability spectrum (Owen, 1970; Brower, Edmunds & Moffitt, 1975; Rothschild *et al.*, 1975; Brower, Gibson, Moffitt & Panchen, 1978) in which some butterflies may be palatable and others distasteful. This spectrum is largely determined by adult encounters with plant sources of cardiac glycosides (cardenolides or CGs) and pyrrolizidine alkaloids (PAs). The former are obtained from larval foodplants (Asclepiadaceae) and the latter through the pharmacophagous behaviour of adult butterflies (for reviews see Brower, 1984; Boppré, 1984; Ackery & Vane-Wright, 1984). A number of deterrent effects have been suggested for these compounds, including the disturbance of cardiac rhythm, emesis, liver poisoning, and bitter taste. Some of them (e.g. emesis) have been demonstrated (Brower, 1984).

Danaus chrysippus thus has the potential to be nasty, as long as the flora it encounters includes the right plants. At Cape Coast, the single most important larval foodplant was *Pergularia daemia* (Gordon, 1982). According to Brower, Edmunds & Moffitt (1975), individual butterflies reared on this species would be sub-emetic for a bee-eater but it would suffer ill effects if it ate three or four of them in quick succession. Chemical analysis of Cape Coast butterflies caught in 1982 reveals CG levels somewhat higher than those found for *P. daemia* butterflies by Brower and his colleagues (Gordon & Gibson, in prep.). PA sources at Cape Coast were common (especially *Crotalaria retusa*) and attracted *D. chrysippus* (especially *Heliotropium indicum*). They presumably contributed to defence and deterrence, but no data are available which would enable an assessment of this contribution.

The evidence thus suggests that the Cape Coast models were nasty, but it should be appreciated that the influence of the local flora may not be decisive. The resident bird fauna includes migrants (notably bee-eaters) whose food preferences and aversions will reflect experiences in other places. Local movements of non-migrants may also be important. In addition, the Cape Coast population of *D. chrysippus* will include immigrants from other areas. Thus both the perceived and the actual palatability spectra may deviate from that predicted from the local flora.

Were predators educated?

Mimics are protected only if predators are educated to avoid the model. This means that models must be common enough for predators to have had experience of their nasty qualities. In the present case there was ample opportunity for the education of predators prior to the irruption of mimics. The average capture rate for *Danaus* in March was 25.7 butterflies an hour (Table 4) as against a peak capture rate for female *Hypolimnas* of 12 butterflies an hour on 1 May (Fig. 3). The sightings data indicate even higher numbers of models in April. In fact, *D. chrysippus* is abundant throughout the dry season (November–April), only becoming scarce as the major rains fall in June and July (Edmunds, 1969, 1976; Gordon, 1982). As mimics are rare in the dry season, there is little chance of predators learning to discriminate between them and models at this time. The stage is thus set for selection for mimicry by the time the rains start.

It is less clear whether or not the subsequent decline in *Danaus* numbers in late May and early June leaves mimics unprotected. Edmunds (1966) assumed

that it would, and interpreted concurrent declines in model numbers and mimic frequencies at Legon (Ghana) in 1965 as evidence for effective mimicry only for as long as models were common. In 1966, however, the decrease in mimic frequencies preceded that in model numbers (Edmunds, 1969). In the present case, formal data on the timing of the latter are lacking, but I would agree with Smith (1976) that the initial correlation observed by Edmunds was fortuitous and that seasonal factors unrelated to predation were responsible. Experimental work suggests that Batesian mimicry can be sustained by relatively few models (Brower, 1960), and Mason, Arzt & Reidinger (1984) have shown that food aversions in red-winged blackbirds are more resistant to extinction than food preferences. They describe this finding as a commonly reported result in the psychological literature.

An ecological model

The interpretation given here provides a general ecological model for intermittent selection by predators that can be tested against field data for *H. misippus*. Population irruptions provoke density-dependent predation which selects for rare and mimetic colour patterns. After the butterflies have (for other reasons?) become scarce, predators switch to more abundant prey. Those phenotype combinations which are both rare and mimetic will be most favoured and will increase in frequency. Rare non-mimics are also likely to increase initially, but will lose their apostatic advantage as they become more common. Provided that *D. chrysippus* remains abundant, mimics will be increasingly favoured as predation is prolonged.

A potentially useful feature of the model is its built-in control against behavioural differences between morphs that might affect the outcome. This control exists since different morphs of *H. misippus* are mimetic in different parts of Africa (Edmunds, 1969; Smith, 1976). Thus the model predicts selection for strong *alcippoides* in Ghana, whereas in Somalia *inaria* should be most favoured.

Elements of the model are supported by two previous studies of *H. misippus*. In two successive years at Legon (Ghana), Edmunds (1969) recorded low survival (*c.* 40%) during and immediately after irruptions, followed by high survival (*c.* 70%) later. In both years, white hindwings (enjoying both apostatic and mimetic protection) had significantly higher recapture rates than orange during the earlier (but not the later) period, and their advantage was greater in the second year when models were considerably more abundant. Edmunds analysed his results separately for fore- and hindwing phenotypes and did not compare the recapture rates of the former for the two periods. In both years, however, *inaria* forewings (enjoying apostatic protection only) had nonsignificantly higher survival rates (*c.* 80%) than *misippus* forewings (*c.* 60%).

In Tanzania, Smith (1976) recorded significant changes in morph frequencies during an exceptionally heavy irruption at Dar-es-Salaam. The data are of considerable interest, since ecological circumstances made the analysis of two discrete generations possible. Following Edmunds (1969), he analysed fore- and hindwing colour patterns separately. In both cases the rarer phenotypes increased, but the increase was most dramatic for the pure *inaria* (oo) forewings. As *dorippus* is the commonest form of *D. chrysippus* in this area, the pure *inaria* forewing enjoys the greatest amount of mimetic protection. It more than

doubled in frequency, from 11.2% in the first generation to 26.8% in the second. White hindwings, enjoying apostatic protection only, increased from 34.2 to 48.0%. Within the first generation, in just over 2 weeks, pure inaria forewings increased from 5.5 to 18.6%. As recruitment to this generation appeared to be simultaneous, this change was probably the result of the differential survival of adults and the overall increase (5.5–28.6%) was closer to five-fold than two-fold. It is clear that strong pressures were involved.

Field data tend to prompt more explanations than they prove, and both Edmunds and Smith offer alternative hypotheses to account for their results. Further application of the selective predation model is required to establish whether or not it has genuine predictive power. It is worth noting that it is not just the mimetic status of *H. misippus* which is being tested. If mimics are protected then the distasteful qualities of *D. chrysippus* are confirmed. These have been questioned, particularly in west Africa (Owen, 1970; Rothschild *et al.*, 1975; Brower, Edmunds & Moffitt, 1975; Brower *et al.*, 1978). Furthermore, the model incorporates three related ecological concepts: density dependent predation, the Type III functional response, and prey switching by predators. These are in turn related to behavioural hypotheses of search image formation and decay in response to the positive and negative reinforcement of predatory behaviour. In so far as the predictions of the model are confirmed, its behavioural and ecological framework is supported.

Evolutionary implications

Batesian mimicry has been described as an “old warhorse” for evolutionary theory (Vane-Wright, 1981), yet its own evolution is not fully understood and the lessons it holds are not exhausted. The jerky selection described here is a reminder that the theory of natural selection makes no firm prediction about evolution rates (Clarke, 1979), even when the requisite variation is present. Evolutionary rates are determined by demographic, developmental genetic, historical and ecological circumstances, rather than by the mechanisms responsible for evolutionary change. Arguments from rate to mechanism are therefore based on a less than compelling logic, although strong conclusions are sometimes reached. Moreover, much of population genetics assumes that selection pressures are constant, an assumption that must often be violated in the real world. We need to know more about the effects of bursts of selection such as those discussed above.

The Cape Coast data also illustrate a frequently overlooked form of balancing selection, that due to epistasis between unlinked loci. The overall frequency of the misippus forewing showed no significant change ($\chi^2_{(2)} = 3.09$, $0.30 > P > 0.20$, for the three periods in Table 2) despite strong selection between phenotype combinations. Its elimination in combination with orange hindwings was presumably offset by its superior survival in combination with white. This helps to explain the rapid restoration of more normal morph frequencies in June and July (Fig. 5). If epistasis of this kind is at all common, it must contribute towards maintaining genetic variation, if only as a buffer against intermittent selection. It also follows that information on microevolutionary processes is lost when attention is limited to single loci. This may

seriously impair our understanding of individual polymorphisms in which epistatic interactions on fitness are difficult or impossible to detect (Lewontin, 1974).

Less generally, the results have a number of implications for our understanding of the evolution of mimicry. First, they show that the selective forces involved can be considerable. On the basis of the morph frequency changes between the second and third periods in Fig. 5, the selective disadvantages relative to good mimics were 73% (*misippus*), 64% (weak *alcippoides*), 42% (*inaria*), and 39% (*inaria-alcippoides*). On the basis of their frequencies in the first and second generations during the irruption at Dar-es-Salaam, Smith (1976) estimated that *misippus* forewings (blw) were at a selective disadvantage of 69% to pure *inaria* forewings (oo). These values may be compared with those of 3–50% observed in the case of *Biston betularia* (Cook, 1976).

Second, apostatic selection and mimetic selection are likely to occur together, and the former may be important in maintaining mimic/non-mimic polymorphisms once mimetic advantage is sabotaged by high numbers of mimics. It will also protect rare non-mimics if predation is intermittent and short-lived (as in the present case). Theoretical studies of mimicry which exclude apostatic selection lead to the conclusion that the fitness of Batesian mimics is number dependent rather than frequency dependent, in that the equilibrium number of mimics depends on the number of models and is independent of the population size of the mimetic species (Charlesworth & Charlesworth, 1975; Turner, 1978). The conclusion no longer holds if apostatic selection is also operative, although it remains true of that portion of fitness due to mimetic advantage.

Third, the results provide fresh support for the theory that the first stage in the evolution of mimicry involves the spread of a mutation with major phenotypic effects (Poulton, 1912; Nicholson, 1927; Turner, 1983). The argument is as follows. The ancestral colour patterns of mimics are frequently so unlike those of their models that major mutations are required before predators can be deceived. These produce fortuitous and approximate resemblances which are subsequently improved by the selection of modifier genes with minor effects. The results described here show that jumping the colour pattern gap is necessary not only to receive mimetic protection but also to get away from the original phenotype. Weak *alcippoides* (especially the blw 1 forms) are so close to the non-mimetic *misippus* that both were predated in May. In other words, mutations with major phenotypic effects reap apostatic benefits that are denied to mutations with minor effects. A similar conclusion was reached by Coppinger (1969) and Ford (1971), although it was expressed in terms of innate avoidance of novel stimuli rather than of apostatic selection.

Fourth, the results support the experimental work of Ikin & Turner (1972) on *Gestalt* perception of prey colour patterns and demonstrate the capacity of predators to select for mimetic supergenes (Clarke & Sheppard, 1960). The disequilibrium in phenotype combinations discussed above was due to the ability of predators to perceive patterns as a whole and to respond accordingly. It resulted from apostatic selection eliminating *misippus* and mimetic selection favouring strong *alcippoides*. The possibility that apostatic selection can affect linkage equilibria as well as individual loci has not previously been

demonstrated. This will exist whenever detectable characteristics of prey species are both polymorphic and determined by genes at different loci.

Fifth, it is often claimed that there is a continuum between Batesian and Mullerian mimicry and that it may be meaningless to attempt to distinguish between them (Huheey, 1976; Sbordoni, Bullini, Scarpelli, Forestiero & Rampini, 1979). Even among advocates of a meaningful distinction, there is pessimism about making it in practice (Sheppard, quoted in Huheey, 1984: 279). Doubts arise because both the palatability of prey and the responses of predators show great variation both between and within species. As a result, individual prey-predator encounters will have different outcomes with respect to prey position on the Batesian-Mullerian spectrum. However, what matters in evolutionary terms is the net response of the predator community as a whole. If this net response is positively frequency dependent (i.e. apostatic), then mimicry is Batesian; if it is negatively frequency dependent (i.e. aposematic) then mimicry is Mullerian (Turner, 1984). On these grounds, and on the evidence reported here, *H. misippus* is a Batesian rather than a Mullerian mimic (*pace* Poulton, 1908; Marsh *et al.*, 1977), and the distinction between the two types of mimicry is theoretically valid and operationally possible.

Finally, changes in the population sizes of mimics may determine the timing and intensity of episodes of predator selection. Although not surprising from an ecological point of view, this conclusion introduces the possibility that a species may be too scarce to evolve mimicry. It also means that selection for mimicry may be intermittent in strongly seasonal species, particularly when specialist predators are lacking. *H. misippus* qualifies in both these respects. The numerous anomalies in the mimicry of this species may be partly due to long periods in which selection for mimicry is absent.

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