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Source: Journal of East African Natural History, 84(1) : 3-18

Published By: Nature Kenya/East African Natural History Society

URL: [https://doi.org/10.2982/0012-8317\(1995\)84\[3:MAOCTI\]2.0.CO;2](https://doi.org/10.2982/0012-8317(1995)84[3:MAOCTI]2.0.CO;2)

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MIMICRY AND OTHER CONTROVERSIAL TOPICS IN EAST AFRICAN LEPIDOPTERA

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INTRODUCTION

Your editors asked one of us (CAC) if he would contribute an article on East African Lepidoptera, particularly relating to the Batesian mimic *Papilio dardanus*. Though it seemed that to write to your Journal about *dardanus* would be like bringing coals to Newcastle, he agreed, provided he was allowed the help of his wife, F.M.M. Clarke, and of I.J. Gordon, who had helped with some of the recent *dardanus* work.

In this paper, we describe the history of some ideas on the evolution of mimicry in butterflies and we explain the contribution of research on *Papilio dardanus* to our understanding of this problem. We also relate our discussion to current controversies in the theory of mimicry, paying particular attention to the ideas of museum scientists in Paris (G. Bernardi and J. Pierre) and London (R.I. Vane-Wright) who have done much to stimulate fresh thinking on the subject. Another area of interest for us over the recent past has been the existence of unusual sex ratios in butterflies and we review our findings on this topic. Finally we show how our early butterfly research led us to a study of haemolytic disease in new born human babies ("Rhesus babies") and helped us to develop a "cure".

MIMICRY

Batesian and Mullerian mimicry

There have been many definitions of mimicry and classifications of mimetic systems (Vane-Wright, 1976; Edmunds, 1981; Endler, 1981; Robinson, 1981; Vane-Wright, 1980), but for present purposes we can define it simply as a resemblance between two or more species which has evolved as a protection against predators, and we only need to consider two types, Batesian and Mullerian mimicry, named after their discoverers (Bates, 1862; Muller, 1878). In Batesian mimicry one of the species is already protected, usually by toxic or distasteful properties, and is called the model, while the other species, which is called the mimic, is edible and is only protected to the extent that it is mistaken by predators for the poisonous model. There is thus a one-way advantage in favour of the mimic. In Mullerian mimicry, however, both species are toxic and/or distasteful and the resemblance is mutually beneficial. This is because individuals of one species may encounter a predator with previous experience of the other species but not of their own. They thus escape an attack which may injure or kill them before the predator realises its mistake.

Batesian mimicry is especially interesting since it has a certain logic that generates testable rules if it is to be effective as an anti-predator strategy. Sheppard (1961) listed these rules as follows:- 1) at least one of the species in a mimicry complex (of two or more species) must be distasteful; 2) the models must be conspicuous so that predators can learn to avoid them; 3) the

models must be abundant enough for the predators to learn to avoid them; 4) the mimics must be encountered by predators which have had experience of the models, which means that the two species should generally be sympatric; 5) the mimics must not be relatively so abundant that the predators only encounter the models infrequently and do not learn to avoid them; and 6) the resemblance between mimic and model must be close enough to deceive the predator on many occasions. Point 5) implies that Batesian mimicry will tend to foster colour pattern diversity or polymorphism, and thus many models may be imitated by a single mimetic species which has several morphs.

All these criteria are usually fulfilled by *P. dardanus* which has different colour pattern morphs each mimicking a different model. Four of these morphs together with their respective models are shown in plate I which has been reprinted from Poulton (1924). Around 13 races of this species have been recognised and the approximate distribution of some of these is shown in figure 1. The males throughout its range are yellow, tailed, non-mimetic and monomorphic, though there are slight differences between races. The many mimetic forms of female, like their models, are all tail-less, the only tailed females being the non-mimetic male-like females in Madagascar and the Grand Comoro, and all the females of race *antinorii* in Ethiopia. Within races there are very clear-cut differences between the forms in the areas where the models occur, but in those regions (such as that occupied by race *polytrophus*) where there are few or no models the mimicry breaks down (Clarke & Sheppard, 1963). In addition to their imperfect mimetic pattern, the *polytrophus* females sometimes have a trace of tails, and even slight tinges of fluorescent yellow male-like pigment.



Figure 1. Approximate distribution of some races of *Papilio dardanus* on the African continent.

We and many others, (Ford, 1936; Clarke & Sheppard, 1959a, 1959b, 1960a, 1960b, 1962) have shown by breeding that the various mimetic patterns of *dardanus* are controlled by genes **at a single locus on a particular chromosome in a definite order of dominance, i.e., a multiple allelic series.** For most of the mimetic forms dominance is complete, **provided that both parents are from the same race.** This complete dominance ensures that maladaptive intermediates (looking like neither model) do not result when the genes for two different mimetic patterns are inherited together: one of the patterns, that controlled by the dominant gene, will be fully expressed while the other, that of the recessive gene, will be completely suppressed.

***Papilio dardanus* and the evolution of mimicry**

Ford wrote in 1936 “The genetics of *P. dardanus* should in the future prove an exceedingly fruitful study...” and so it has—no sooner is one problem solved than another rears its head. As Ford anticipated, research on *dardanus* genetics has helped to shape our current understanding of the evolution of mimicry. In order to put this research (and some current controversies) in context, some background on the history of ideas on the evolution of mimicry is necessary.

Mimicry is now so strongly identified with classic Darwinian evolutionary theory that it is hard to appreciate that it was once seen as evidence against natural selection as a creative force in evolution. Yet in 1915, R.C. Punnett published a book on the subject, which was a sustained attack on the power of natural selection to produce complex adaptations. The problem was one that had haunted Darwin himself—that of the maladapted intermediate form or the apparently bridgeless gap. In many cases it was clear (from phylogenetic comparisons) that ancestral colour patterns were totally unlike present day mimetic patterns. How could the gap between the two be bridged if there was gradual evolution as Darwin had claimed? A small change in the ancestral pattern of the mimic might be a shift in the direction of the pattern of the model but would fall far short of producing convincing mimicry and hence could not be selected for this reason. Only a major change could accomplish a protective resemblance.

Darwin was of course deeply committed to the idea of gradual evolution, and he argued that both model and mimic were originally similar-looking, dull-coloured butterflies. Subsequently, as the model developed distasteful properties, so it gradually acquired a warning colour pattern, and the mimic tracked its evolution in a likewise gradual manner.

Punnett attacked Darwin's theory on two important grounds. First, it was hard to apply to cases where different mimetic species (with non-mimetic males) resembled the same model. It was generally believed, on the basis of phylogenetic comparisons, that the non-mimetic male patterns in Batesian mimics were ancestral. Punnett pointed out that these male patterns were often very different in mimics which shared the same model. If Darwin's theory was correct and if they were indeed ancestral, then they should all have resembled the ancestral model pattern and therefore should have looked alike. Second, breeding experiments with two mimetic species (*Papilio polytes* and *Hypolimnys dubius*) showed that no intermediates resulted when different mimetic forms were crossed. Instead the various patterns segregated cleanly, showing no evidence of the genes with small effects whose presence was predicted if mimicry had evolved in the manner suggested by Darwin.

Punnett's book was published at a time when there was bitter controversy between those who believed, like Darwin, that evolution was gradual and was driven by natural selection working on genes of small effect, and those, following new discoveries in genetics, who believed that evolutionary changes were sudden and were driven by mutations with large effects. He (Punnett) belonged to the latter camp and he argued that the absence of mimetic intermediates should be taken at face value and as evidence that complex features of organisms could and did arise at a single step. He suggested that this was not implausible since model and mimic would share common genes for colour patterns inherited from common ancestors, and

that mimicry could arise by activation in the mimic of the same genes that existed in the model. Punnett's views were later revived by Goldschmidt (1945) who stressed that butterfly patterns were constrained by a few basic developmental pathways that could be independently reproduced by different or recurrent mutational events.

Under Punnett's and Goldschmidt's theories, natural selection merely increases the frequency of an already perfect mimetic form; it does nothing to build up the resemblance itself. The creative power of natural selection is therefore denied; it is the mutation that makes the masterpiece, not natural selection. It is not surprising that this view was opposed by those who were convinced that only selection could make sense of the apparent design of living organisms, and who could not believe that detailed mimicry could be produced by a single, random mutation. Amongst the latter were E.B. Poulton, A.J. Nicholson, R.A. Fisher and E.B. Ford. The ideas of these authors on the subject of mimicry have since been conflated into what is known as the two-phase theory. Turner (1983a), in a most intriguing paper, argued that Fisher's theory was somewhat different and has been "consistently misdescribed" to conform to what is now the classic theory of the evolution of Batesian mimicry.)

According to the two-phase theory, an initial mutation with a major effect on the colour pattern gives a rough and ready resemblance to a protected species and spreads. It spreads because of a tendency by predators to generalise, especially when experiences are unpleasant, so that anything which looks vaguely like the model is avoided. The second phase begins once the initial mutation has become well established. In this phase, there is selection for modifier genes on different chromosomes which have minor effects on colour pattern which perfect the mimicry. This selection occurs because some predators are more discriminating than others and learn to attack the less perfect mimics.

A key difference between the mutation theory and the two phase theory is that the latter predicts the presence of modifier genes while the former predicts their absence. We tested these predictions using *P. dardanus*. This proved to be an ideal butterfly to use since some of its 13 races (*humbloti* on the Comoros Islands, *meriones* in Madagascar; fig. 1) have apparently failed to evolve mimicry, with the females resembling the males both in colour pattern and in the presence of fully developed tails. Now, if mimicry had never evolved in *humbloti* and *meriones*, then it follows that modifier genes for better mimicry should be absent in these races. Clearly therefore, if the two-phase theory was correct, a gene that would produce good mimicry in one of the mainland races, where modifiers were present, would fail to do so in the island races from Madagascar and the Comoros, where modifiers are absent. If, on the other hand, Punnett and Goldschmidt were correct, it would still produce the perfect mimetic pattern in all its detail, doing this by activating shared, ancestral gene/development pathways.

Together with the late Philip Sheppard and with the help of many collaborators in East Africa (including members of the EANHs), we arranged for the collection and shipment of live *dardanus* from both the mainland of Africa and from Madagascar, and we hybridised them in Liverpool. We were able to do this by using the technique of hand mating (Clarke, 1952). The results were unequivocal, with hybrids between different races showing a breakdown in mimetic colour patterns despite the evident presence of the genes for mimicry (Clarke & Sheppard, 1963). This was good evidence that mimicry had evolved according to the two-phase theory.

When one looks at the end result of all this research and at the array of models and mimics shown in all the butterfly books, Batesian mimicry to us sounds both incontrovertible and also extremely complicated. Some very intelligent people do not believe in it at all, and some who do believe in mimicry think that the mimics were there first and that the non-mimetic male colour patterns of *dardanus* were not ancestral but arose later in evolutionary time. If the mimics were there first, then our interpretation of the hybrid work is thrown into question.

Several difficulties arise. Our assumption that mimicry never evolved in *humbloti* and *meriones* would be wrong; we could no longer maintain that modifiers are necessarily absent in these races; and the core idea that mimetic patterns have a selective advantage relative to male-like patterns would be over-turned since the latter would have replaced the former in Madagascar and the Comoros.

A French view of mimicry

In the opinion of the French scientist Bernardi the classical theory of Batesian mimicry in *P. dardanus* has been completely disproved. He and his colleagues describe most fully all the female forms of *P. dardanus* and their distribution in Africa, and they point out that for a very high proportion of them there are no models, and furthermore in some areas non-mimetic forms fly with mimetic ones and would be expected to be strongly selected against (Bernardi, Pierre & Nguyen Thi Hong, 1985). Bernardi (1963) has also argued strongly that, since the mimetic colour patterns are morphologically primitive in comparison with the male colour patterns, then they must be ancestral. He believes that though the mimetic forms do obtain some protection from their mimicry, the development of the wing pattern was not due to this but to convergent and/or parallel evolution. In convergent evolution similarities of form evolve independently in different species because they become adapted in similar ways to living in similar types of environment. In parallel evolution, similarities arise because different species share similar genes and developmental pathways which can be independently modified, suppressed or re-activated to produce similar results. To the extent that they invoke parallel evolution, the views of Bernardi and his colleagues are reminiscent of those of Punnett and Goldschmidt.

Vane-Wright (1978, 1979) agrees with Bernardi on the question of the ancestral states of male colour patterns and writes "The general acceptance of the idea that the male form of *P. dardanus* Brown is ancestral dates back to Trimen's (1869) inspired speculations about this highly polymorphic species. But as pointed out earlier by Bernardi (1963.....) on the basis of the comparative anatomy of butterfly wing patterns, the mimetic forms of *P. dardanus* are closer to a primitive condition than is the male pattern, which appears to be highly specialised. I am completely in agreement with Dr. Bernardi on this point, and that the male-like female represents the "phase finale" of female evolution in this species" (Vane-Wright, 1979). Bernardi thinks that this new interpretation is generally accepted by the "English team grouped round Vane-Wright".

Vane-Wright and Smith (1991) carry the argument further with a species-level cladistic analysis of the phylogenetic relationships between *Papilio phorcas*, *P. dardanus* and *P. constantinus*. They point out that the idea that *P. dardanus* is closely related to *P. nobilis* (which resembles male *dardanus*) has been completely discredited. It follows that the resemblance between them cannot be taken as evidence that the pattern of the latter is primitive (pace Turner, Dearney & Exton, 1984). Further, as pointed out earlier by Vane-Wright (1978), the total lack of resemblance between the males of *P. phorcas* and *P. dardanus* implies considerable evolutionary changes in their patterns since these sister species split from their common ancestor. However, the cladistic analysis of Vane-Wright and Smith does not extend to the subspecies within *dardanus* other than as a series of unresolved hypothetical cladograms, and, as they point out, such an analysis is crucial to the resolution of ancestral colour pattern states within *dardanus*.

Further evidence for the views of Bernardi and Vane-Wright comes from the *antinorii* race of *P. dardanus* which is found in Ethiopia. Here there are male-like female forms which are genetically dominant to the mimetic forms and all the females have tails. In crosses between mainland African stock and race *antinorii*, unlike those between Madagascar and Comoros

racess with mainland stock, the tails in the females are sometimes dominant. These are puzzling facts since we generally expect ancestral forms to be recessive. The reason for this is that it is hard for recessives to be selected for their advantageous qualities since they are rarely expressed at low frequencies. This means that where we have a dominant and recessive allele at any locus, it is much more likely that the dominant allele is the more recently evolved since its chances of spreading under selection would have been much greater. Where there is a series of alleles the order of dominance should reflect the sequence with which the alleles have appeared in evolutionary time. The situation in *antinorii* thus suggests that tails and male-like female colour patterns are derived and not ancestral.

We accept that problems remain with the classical interpretation of mimicry in *P. dardanus* (especially with respect to the dominant male-like female forms), and that further investigation (particularly at the DNA level) is necessary (Clarke, Gordon, Smith & Vane-Wright, 1991), but we are not yet convinced by the views of Bernardi and Vane-Wright for the following reasons.

First, if the theory of mimicry is correct, then arguments based on morphologically primitive and derived states in mimetic colour patterns are irrelevant to the point at issue because they cannot decide it. In Batesian mimicry, the mimic is wearing borrowed clothes. Whatever characteristics the model has, whether primitive or advanced, they will be "copied" by the mimic and will be secondarily derived in that species. The pertinent question is therefore not "Why are mimetic colour patterns primitive?" but is instead "Why are model colour patterns primitive?". Interestingly, classical theory suggests an answer: models are subject to conservative selection for colour pattern (since deviations will not be recognised by predators as distasteful) and so are expected to retain ancestral colour patterns. To put this same point somewhat differently, the observation, that mimetic colour patterns in females are morphologically primitive relative to male patterns, can be explained in two ways: one, by the classical theory of Batesian mimicry and warning colouration, or, two, by the hypothesis that the male patterns evolved later than the female patterns. The observation is interesting, but it is not evidence against the classical theory.

Second, despite the confused dominance relationships of the hindwing tails, their presence in female *P. dardanus* is almost certainly an ancestral feature, while their absence is derived and is clearly associated with mimicry. As already noted, the females of some races of *P. dardanus* have tails, as do the two closest living relatives of this species, *P. constantinus* and *P. phorcas*, and many other members of the genus. If lack of tails in female *dardanus* is the ancestral condition in this species, then it means that tails would have had to have first been lost (in the lineage leading to ancestral *dardanus*) and then regained (in the lineages leading to *antinorii*, *meriones* and *humbloti*). While not impossible, such an hypothesis violates the criterion of parsimony which requires that the simplest explanation is preferred when reconstructing evolutionary histories. In the species-level cladistic analysis of *dardanus*, *phorcas* and *constantinus* presented by Vane Wright and Smith (1991), tails are not among the characters used, although their doubly reversed evolution (loss and regain) is proposed in a hypothetical pathway for subspecies evolution in *dardanus*.

Third, the rule (called "Haldane's Sieve" by Turner, 1983b) that correlates order of dominance with order of appearance in evolutionary time is statistical, not absolute, since there can be reversals of dominance, since recessives can spread if they are associated with heterozygote advantage, and since chance, operating through genetic drift and founder effects, can also increase the frequency of rare recessives to the point when their phenotypes are expressed. Exceptions to the rule are predicted, so we should not be surprised to find them in *P. dardanus*. It is interesting in this context that a recent examination (Brower, 1995) of mitochondrial DNA in *Heliconius* butterflies casts considerable doubt on wing-pattern phylogenies derived by using Haldane's Sieve (Sheppard, Turner, Brown, Benson & Singer,

1985). It may turn out in the end that the "holes" in Haldane's Sieve are much larger than had been thought, and that recessives are not uncommonly more recently evolved than dominants: if this is the case, a great deal of agonising over *P. dardanus* will have been quite unnecessary!

The persistence of non-mimetic forms

As noted above, Bernardi *et al.* (1985) have drawn attention to the extensive occurrence of non-mimetic female forms in those races of *P. dardanus* in which mimics are present. A similar situation exists in another well-known example of Batesian mimicry, the diadem butterfly, *Hypolimnas misippus*. In this species there are four different colour forms which show impressive resemblances to four corresponding colour forms in the distasteful danaine butterfly *Danaus chrysippus*, but whereas the latter is monomorphic over large areas of Africa, the former is polymorphic everywhere with the result that mimics are found thousands of miles outside the range of their presumed models (Pierre, 1973, 1980). For example in West Africa only one form of the model occurs (*f. alcippus*) but all four forms of *H. misippus* are found so that three of them are effectively non-mimetic in this area (Edmunds, 1969). Worse still for the theory of mimicry, the one mimetic form (*f. alcippoides*) is relatively rare. Not surprisingly, Bernardi and his co-workers are also sceptical about mimicry in this species (Bernardi, 1963; Pierre, 1973, 1980). How do non-mimics persist together with mimics if the latter are at an advantage as claimed by classical theory?

There are two standard answers to this difficulty, which can both be illustrated with reference to the puzzling case of *Hypolimnas misippus*. The first is related to the fact that predation is usually positively frequency dependent since the commonest forms of a prey species are more easily recognised by predators because they are encountered more frequently. Indeed, as recognised in the rules for Batesian mimicry, if a mimic becomes too common relative to its model then the colour pattern they share will become associated with edibility rather than distastefulness and all advantage to the mimic will be lost. Even if this does not happen, rare non-mimics may be encountered too seldom to be attacked. There is field evidence that this is the case in *H. misippus*: during a period of low survival in a mark-recapture study in Ghana, common non-mimics decreased significantly both in frequency and in recapture rate, mimics increased significantly in frequency and maintained their previous recapture rate, while rare non-mimics showed no changes in either parameter (Gordon, 1987). The mere presence of non-mimetic forms is therefore not strong evidence against mimicry.

The second answer is that predation is only one of several selective forces that operate on butterfly colour patterns. Sexual selection may favour one pattern over another and different thermal properties of absorption and reflectance may also affect their relative fitness. It is also usually the case that genes have multiple (pleiotropic) effects, so that a gene for a mimetic pattern might also, for example, affect physiology or fecundity. Moreover, genes are often linked together in tightly knit groups (supergenes) on the same chromosome, so that they are nearly always inherited together as a single unit. A gene for a mimetic colour pattern might therefore be associated with genes for other effects and selection for these effects may be stronger than selection for mimicry. It is likely that this is the case with the gene for hindwing white in *H. misippus*, which is associated with reduced body size (Gordon, 1982). All of this means that the frequency of a gene for mimicry will be determined by a balance of diverse selective forces and the overall result may be that it remains rare despite its general advantage vis-a-vis predation.

What the persistence of non-mimetic forms shows, therefore, is not so much that classical mimicry theory is wrong, but that it is seldom the whole story. In the case of *P. dardanus*, this

will surprise no-one who has looked at a museum drawer full of its bewildering array of female forms of which only some are obvious mimics.

The Monarch and the Viceroy: Does nature deceive?

The muddle over Batesian—and indeed Mullerian mimicry as well—is exemplified by an article, leader and subsequent correspondence in two 1991 issues of *Nature* dealing with the relationship of the Monarch butterfly (*Danaus plexippus*) to the Viceroy (*Limenitis archippus*). This relationship has classically been interpreted as an example of Batesian mimicry with the former as the model. The article (Ritland & Brower, 1991) suggested that the Viceroy was in fact as unpalatable as its model the Monarch and, if so, this implied that the two similar looking butterflies were Mullerian, not Batesian, mimics.

The leader in the same issue of *Nature* (Vane-Wright, 1991) pointed out that opponents of Darwinism have always tried to discredit Bates' idea and that although this survived (because it explains the facts better than any other alternative) it has been marginalised and Batesian mimicry is now often seen as little more than an intriguing evolutionary side-show, part of the "genteel upper-middle-class fascination with snails and butterflies" as Richard Lewontin once put it (Lewontin, 1974). Vane-Wright went on to cast doubt on the widespread occurrence of Batesian mimicry suggesting that it is too unreliable to be effective and arguing that chemical defence is more likely to evolve because it is a better protection. Quoting from Rousseau, he suggested that nature does not deceive, it is only we who deceive ourselves.

The article and the leader led to a vigorous correspondence. Guilford (1991) wrote to argue in favour of the Batesian mimicry of *archippus* because of subtle differences of taste between it and *plexippus*. Rothschild (1991) pointed out that as long ago as 1958 Jane Brower had concluded that *archippus* was neither a Batesian nor Mullerian mimic in the classical sense and that *archippus* contains a high proportion of carotenoids, characteristic of models rather than mimics. Together with Marsh, we wrote (Clarke, Clarke, Gordon & Marsh, 1991) that we were not aware of any evidence that chemical defence is more likely to evolve than a Batesian type of mimicry, while evolution is opportunistic and must make do with the genetic variation that is to hand, and this may be an alteration in colour pattern rather than in chemistry.

Like many of the other controversies surrounding mimicry, the dispute in *Nature* was a revival of old arguments which have never been fully resolved. The existence of both forms of mimicry has been challenged at various times and there have been many semantic disputes over whether deception is involved or not. Early objectors (e.g. Punnett, 1915) to the idea of Batesian mimicry drew attention to the paucity of records of birds attacking butterflies, and more recently Rothschild (1980) has argued that almost all day-flying Lepidoptera are distasteful to some degree and that this is almost a *sine-qua-non* for day-light activity in such conspicuous insects as butterflies, claiming, like Vane-Wright, that most mimicry is Mullerian.

Others (Wickler, 1968; Huheey, 1976) have argued that there is always an element of Batesian mimicry and deception in Mullerian mimicry, since the two species involved are seldom likely to be equally distasteful to all predators or equally numerous, so that there will be times when a less distasteful species is avoided because the predator mistakenly believes it to be the more distasteful. Furthermore, variation in distastefulness occurs not just between species but also within them. Some butterflies (such as the danaines) obtain their chemical defences from plants, and these characteristically show a palatability spectrum with some individuals highly protected and others not at all, depending on the plants on which they have fed (Brower, 1984). As if all of this variation were not enough, there is also the factor of predator appetite, with starving individuals eating food that less hungry ones would avoid.

The standard means of resolving these issues is a combination of chemical investigations which characterise and quantify the chemical defences involved and laboratory experiments

which test the responses of captive predators to the prey items in question (Brower, 1984, and references therein). Such investigations have been very fruitful, but they do not tackle the issue of what actually happens in the field, and, by focusing on individual interactions, they add to the difficulty of seeing the wood for the trees. In evolutionary terms what matters is the overall outcome of interactions between natural populations of butterflies and their predators, something which might seem hard to determine.

There is, however, a way forward, though it may only be applicable in a few instances. This takes advantage of the differing outcomes of frequency-dependence when predators are feeding on distasteful or palatable prey (Turner, *et al.*, 1984). In the case of distasteful prey, predation is negatively frequency-dependent, *i.e.* the rare forms are more frequently attacked because they are less likely to be recognised as bad to eat. In the case of palatable prey, as noted above, the reverse is the case with positive frequency-dependence being the rule and the commonest forms being most attacked as they are most likely to be recognised as good to eat. So if frequency-dependent predation on natural populations of mimics can be detected, then it is possible to determine whether on balance they are palatable or distasteful and hence whether they are Batesian or Mullerian mimics.

Using this criterion, both Mullerian (Benson, 1972) and Batesian mimicry (Gordon, 1987) have been distinguished in the field. In Benson's study the colour patterns of butterflies in a natural population of a suspected Mullerian mimic (*Heliconius erato*) were altered artificially and the individuals were marked and released. Recapture data indicated lower survival rates for the rarer of the artificially altered individuals, as expected if the species was distasteful and its mimicry is Mullerian. In Gordon's study, as noted above, the commonest forms of *H. misippus* had significantly lowered recapture rates in comparison with rarer forms and also declined in frequency. Other evidence (morph frequency changes and linkage disequilibrium) was consistent with the interpretation that the lowered survival was a consequence of predation on common non-mimics, indicating that the species is palatable and its mimicry is Batesian.

On a more subjective level, some naturalists have had no problems distinguishing between the two types of mimicry. In reply to a suggestion from Poulton, Marshall (1902) wrote "I cannot at present accept your suggestion that *Hypolimnas misippus* is itself protected..... in these matters I depend more than anything on the habits and actions of the insects as I have seen them when undisturbed and when frightened (there) is to my mind a radical difference between mimics and their models ... which is often hard to define. There is also a structural difference which appeals to me so that I believe I could almost tell one from the other with my eyes shut merely by the feel of it in the net." Indeed, there may be whole suites of adaptations associated with being palatable or toxic, ranging from roosting habits (single vs. gregarious, and early vs. late), resistance to injury and wing fragility (fragile vs. tough), female mating frequencies (once or twice vs. many), longevity (short vs. long), response to attack (panic and rapid protean flight vs. thanatosis [playing dead] and relaxed flight, see Edmunds 1974), and normal flight patterns (usually more rapid and wary vs. slow and sailing). These can provide clues that are useful when direct evidence on palatability is lacking.

UNUSUAL SEX RATIOS

Although equal sex ratios are the general rule in butterflies and moths, a number of interesting exceptions are known. They include the East African butterflies *Danaus chrysippus*, *Acraea encedon*, and *Acraea encedana*, and the Asian and Pacific butterfly *Hypolimnas bolina* (also found in Madagascar). In most Lepidoptera, sex is determined by an XY system, but, like birds and unlike mammals, it is the female sex which is heterogametic (XY) and not the male. If the

female produces gametes carrying unequal frequencies of the X and Y chromosomes (segregation distortion), then unequal sex ratios will be observed in the offspring. Unequal adult sex ratios can also result if there is differential survival of immature stages with XY and XX chromosome complements.

The first report of distorted sex ratios in an African butterfly was by Poulton (1914) who described all-female broods in *Acraea encedon* reared in Nigeria by W.A. Lamborn. Little attention was paid to this result until Owen (1965) discovered *A. encedon* populations in Uganda in which males were rare with frequencies of under 2%. Subsequently, Owen (1970) showed that there were strains of females in this species which never produced male offspring. Following a suggestion by Hamilton (1967), and because there was no difference in brood size between unisexual and bisexual broods, he proposed that these unisexual broods were due to the inheritance of a Y-linked gene which caused non-random segregation of the sex-chromosomes during meiosis, with the eventual result that the Y chromosome always ended up in the cell which produced the egg. This is known as meiotic drive and the Y chromosome which shows meiotic drive is called a driving-Y chromosome. Driving-Y chromosomes are of considerable interest, since their existence is predicted by selfish gene theory (Dawkins, 1982), and since their presence can eventually lead to the elimination of the homozygotic sex and thus to the extinction of the species (Hamilton, 1967).

Further work in Uganda by Owen and Chanter (1968) showed that all-female broods were also present in another African butterfly, *Danaus chrysippus*, a result which was subsequently confirmed for this species in Tanzania (Smith, 1975). Smith demonstrated matrilineal inheritance of the all-female trait in *D. chrysippus* through five generations, although in other lineages there were reversions, and he followed Owen in attributing the all-female broods in this species to a driving-Y chromosome. Gordon (1984) subsequently demonstrated the presence of all-female broods in *D. chrysippus* in Kenya, and, following Owen and Smith, accepted meiotic drive as the probable explanation.

We (CAC and Philip Sheppard) were sceptical of the driving-Y chromosome theory, since its mechanism appeared improbable to us, and since there is always so much variance in brood sizes. We therefore decided to investigate the problem in another species of butterfly, *Hypolimnas bolina*, in which all-female broods (reared by H.W. Simmonds) had been reported from Fiji by Poulton (1923). We (Clarke, Sheppard & Scali, 1975) applied a highly useful cytogenetic technique discovered by S.G. Smith (1945). Smith showed that in the Spruce Budworm moth (*Archips fumiferans*, a pest of pine trees) all the somatic cells in females possessed a heteropyknotic body whereas males lacked it, and Traut and Mosbacher (1968) found the same to be true in most species of Lepidoptera. The Smith body was later shown to be an inactive section of the Y chromosome, and this is of great interest in relation to the situation in mammals, where there is also a heteropyknotic body in the somatic cells of the female (the Barr body) but here it is one of the two Xs, either maternal or paternal, which is inactive over most of its length.

We have been able to detect the Smith body in both eggs and caterpillars and in the latter case we have done so without killing the caterpillar by the removal of an abdominal proleg. After amputation each caterpillar is kept separately and cotton wool applied to the wound. The caterpillars recover, and there is no deformity in the perfect insect. In the adult, gut or Malpighian tubule cells are used from freshly killed insects. The tissues are stained with orcein and a coverslip placed on the slide to make a squash preparation. By following these procedures we were able to show that the Smith body is accurately diagnostic of sex in *bolina*, and that males are present in all-female broods but that they die either as embryos or as small larvae. Simmonds (1930) had observed that a large percentage of the eggs in all-female broods

in this species failed to hatch and our result strongly suggested that these were males and the all-female trait is due to a cytoplasmically inherited male-killer factor.

The *bolina* result prompted a re-evaluation of the meiotic drive hypothesis in *D. chrysippus*. In a large scale breeding programme in Zimbabwe, one of us (IJG) recorded egg and caterpillar mortality in unisexual and bisexual lines bred from wild butterflies from Tanzania, Kenya, Zimbabwe and Ghana. The results were clear: overall survival rates from egg to adult were twice as high (75.4%) in bisexual broods as in the all-female broods (38.6%). Most of the mortality occurred in the eggs, which failed to hatch despite the presence of a fully developed first instar larva. This result strongly suggests that unisexual broods in this butterfly result from the early death of males, usually just before hatching from the egg.

The reasons why the males die, however, remain uncertain. We (Clarke, *et al.*, 1975) had originally suggested that an infective agent might be the cause in *H. bolina*, as in all-female broods in *Drosophila* where spirochaetes and viruses have been implicated (Oishi & Poulson, 1970). However, tests for viral particles and spirochaetes were both negative. Gordon (1984) suggested that all-female broods and aberrant autosomal segregations in *D. chrysippus* might be due to the hybridisation of previously isolated geographical races, and predicted the absence of these odd genetic events outside East and Central Africa. Smith (1976, 1980) had earlier invoked previous episodes of allopatric evolution in African populations of *D. chrysippus*, in order to explain the otherwise puzzling colour pattern polymorphism in this distasteful species. Smith, Owen, Gordon & Owiny (1993) present additional evidence from Uganda for the hybridisation hypothesis, and more recently, Smith and Owen (in press) have described large-scale migratory behaviour in *D. chrysippus*, pointing out that this would lead to hybridisation over the large areas of East and Central Africa (Uganda, Kenya and Tanzania) in which polymorphism and unisexual broods are found.

In both *D. chrysippus* and *H. bolina* (which is also migratory), the geographical distribution of all-female broods is restricted to certain areas. It would be interesting to investigate the hybridisation hypothesis experimentally in both species by appropriate crosses between geographically isolated populations in which all-female broods are unknown. In *D. chrysippus*, they are only known from East and Central Africa, and in *H. bolina*, they are known from Fiji, Sri Lanka, Sarawak and Hong Kong, but appear to be absent from Papua New Guinea and Australia. This species also occurs in Madagascar but we do not know whether all-female broods occur there or not. There is clearly scope here for further work of the same nature that shed light on the evolution of mimicry in *P. dardanus*.

The rejection of meiotic drive as an explanation for all-female broods in *D. chrysippus* suggests that this hypothesis should be re-examined in *A. encedon*. Owen, Smith, Gordon & Owiny (1994) note that this species is likely to have shared, with *D. chrysippus*, a similar African Pleistocene history of alternating periods of allopatric evolution and hybridisation. Moreover, like *D. chrysippus*, it is highly unusual for its family, and is theoretically anomalous, in being simultaneously distasteful and polymorphic for colour pattern. As Owen *et al.* point out, it is therefore feasible that all-female broods may also be due to hybrid breakdown in *A. encedon*. Such an hypothesis will, however, have to explain why all-female broods in this species, together with colour pattern polymorphism, appear to be found throughout Africa (having been reported from Tanzania, Uganda, Sierra Leone, Ghana and Nigeria) rather than just in a zone of overlap in East and Central Africa. Since *A. encedon*, unlike *D. chrysippus* and *H. bolina*, is not a migrant, this poses a real difficulty for a parallel explanation for the origin of all-female broods and colour pattern polymorphism in this species. Furthermore, in contrast to the situation in *D. chrysippus* (where aberrant autosomal segregations and assortative mating [Smith, 1984; Gordon 1984] for colour patterns are common), there is no independent evidence for allopatric evolution and hybridisation in *A. encedon*.

There are other unresolved difficulties, including the fact that the sizes of all-female and bisexual broods in *H. bolina* are similar, as was observed by Owen in the case of *A. encedon*. This may be because of density-dependent mortality in laboratory stocks or because the mothers of all-female broods lay more eggs than do those of bisexual broods.

A further curiosity is the high frequency of females carrying the all-female trait in some natural populations. In *D. chrysippus* on the Athi Plains near Nairobi, this frequency can reach 83% or more. In *A. encedon* at Newton in Sierra Leone, 50 out of 53 wild females produced all-female offspring, giving a frequency of over 94% for the all-female trait (Chanter & Owen, 1972). Obviously the dynamics of the trait will be quite different if it is due to meiotic drive than if it is due to a cytoplasmic male-killer or to hybrid breakdown. Other things being equal, in the case of meiotic drive, it will spread to fixation, while in the case of a cytoplasmic male-killer the trait will be selectively neutral despite its lethal effects on males (because it is only inherited through the female line). In the case of hybrid breakdown, trait dynamics will depend on a complex mixture of evolutionary history, mating behaviour, natural selection, chance and migration.

A possible influence on trait dynamics is kin selection. Kin selection occurs if male deaths release resources for use by female siblings and if these extra resources improve their survival. Hurst (1991) has shown with a simple mathematical model that a cytoplasmic male-killer can invade a population and will reach equilibrium frequencies if kin selection is operating. This could certainly be the case in *A. encedon*, since these butterflies lay their eggs in batches and siblings may end up competing for food, but it seems less likely in *Danaus* and *Hypolimnas* which lay their eggs singly.

It is clear that all sorts of questions arise with regard to the evolutionary origin and current dynamics of sex ratio distorters in east African butterflies and naturalists in this region are extraordinarily well-placed to contribute to our knowledge of this fascinating problem in evolutionary history, genetics and ecology.

BUTTERFLY GENETICS AND PREVENTING RHESUS BABIES

Breeding butterflies and moths used to be an easy way to learn genetics, though agreed it cannot compete with all the intricacies which have been demonstrated in *Drosophila*. Nevertheless butterfly genetics has produced a medical "first", for it was a study of mimicry which led to a very effective prevention of "Rhesus" babies and here, as a finale, follows the sequence of events which culminated in the "Liverpool jab". "Rhesus" babies result when a Rhesus-negative mother becomes immunised against Rhesus positive blood cells. This occurs when foetal blood cells from a Rhesus positive baby (the Rhesus positive factor coming from a Rhesus positive father) leak across the placenta at or just before delivery and stimulate production in the mother of anti-Rh antibodies. These then attack and destroy the blood cells of any subsequent foetus carrying the Rhesus positive blood group. Such Rhesus babies may either be aborted or die shortly after birth, and could formerly only be saved by a total blood transfusion immediately after delivery.

Following our initial studies of the genetics of *P. dardanus*, we decided to look at mimicry in *P. memnon* which has much in common with that of *P. dardanus*. Mimicry in this species is also shown only by the female, and superficially it also appears to be controlled by a series of alleles at a single autosomal locus which is sex-limited in its expression. These alleles produce the different female forms, one of which is tailed and several are tailless. However, in our breeding work and in other collections we have come across some remarkable insects which strongly support the view that the "multiple alleles at a single locus" theory is wrong, and that

the true explanation is that the mimetic pattern is controlled by a series of closely linked genes all on the same chromosome and usually inherited as a unit (probably true also in *dardanus*). In such a situation, crossing over occasionally occurs, producing butterflies with mixed features (Clarke, Sheppard & Thornton, 1968). For example we bred a female f. *achates* which has the usual long tails and *achates* wing pattern, but had a black instead of a yellow body. There have also been several other recombinations of pattern, one very remarkable one in which the usually tail-less f. *butlerianus* has gained long tails.

It was this mechanism of crossing over within a supergene, together with the interactions of colour pattern genes with sex and with modifier genes that exist in both *dardanus* and *memnon*, which led to our interest in the Rhesus blood groups. We realised that there were fascinating parallels between the genetics of these quite different traits. In Rhesus blood groups, as in swallowtail colour patterns, occasional crossing over within a supergene results in new combinations of the Rhesus factors which affect the probability of haemolytic disease occurring. Further, in Rhesus blood groups, as in swallowtail colour patterns there is interaction with other genes. One of the most interesting and important of these interactions is that between the Rhesus genes and those responsible for the ABO blood groups which results in a reduced incidence of haemolytic disease when there is ABO incompatibility between mother and foetus.

Our interest in the Rhesus-ABO interaction in particular gradually led to ideas about how to prevent Rhesus haemolytic disease. We (CAC and FMMC) suspected that the reduced incidence of the disease was due to the mother's anti-A or anti-B destroying leaked foetal blood cells before any maternal anti-Rh has a chance to develop. This led to the idea that we could do the same thing by giving anti-Rhesus antibody to an Rh-negative mother to get rid of any Rh-positive foetal cells (Clarke, 1967). It worked miraculously, as soon as we began giving the correct antibody, i.e. the 7S 'coating' type, and not the 19S agglutinating form which we used first (on the advice of experts) and which failed. Our critics, when hearing of our initial mistake, said 'I told you so'. However, the 7S is now standard practice and is given to all non-immunised Rh-negative women who have just had an Rh-positive baby and the young obstetricians can now sleep quietly in their beds (Clarke & Hussey, 1994). For a recent general survey of the whole story see Clarke (1989).

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