

## Aposematic polymorphism in the tropical butterfly *Danaus chrysippus*: A review

Eihab Idris<sup>1\*</sup>

<sup>1</sup> Department of Zoology, Faculty of Science, University of Khartoum, P.O. Box 321, Postal Code 11115, Khartoum, Sudan.

\* E-mail: eihabidriss@gmail.com

### ABSTRACT

In theory, the selective attacks by experienced predators are expected to drive aposematic prey species towards colour monomorphism because mutant individuals with divergent colour forms will not be recognized as distasteful and thus will be targeted by predators. The tropical butterfly *Danaus chrysippus* represents a notable exception to this rule since it is aposematic but shows extensive colour pattern polymorphism in the region of East and Central Africa. In this paper, we present a critical review of the various hypotheses that were suggested to explain the origin and maintenance of colour polymorphism in *D. chrysippus*. Three different approaches to this problem were revised and criticized: first, that polymorphism is a non-adaptive consequence of past geographic isolation that resulted in the formation of a hybrid zone, second, that polymorphism represents an evolutionary escape route when an aposematic colour form is heavily loaded by batesian mimics and third, that polymorphism is maintained because *D. chrysippus* is subjected to spatially and temporally variable Müllerian selection as a result of recurrent population extinctions in the mimetic *Acraea* species, driven by the spread of the male-killing *Wolbachia* bacterium. It has been argued that the three hypotheses are not mutually exclusive; alternatively, each hypothesis targets a distinct problem and exploits a distinct set of key observations. The study concluded that the final solution to the long standing problem of aposematic polymorphism in *D. chrysippus* might be achieved through the adoption of a pluralistic approach that integrates all the three hypotheses.

**Keywords:** Hybrid zone, Müllerian mimicry; Batesian mimicry; Metapopulation dynamics; *Spiroplasma*; *Acraea*; Africa

### INTRODUCTION

Aposematic species are those species that combine warning coloration with tissue inedibility in order to deter potential predators (Barnard, 2004). The evolutionary theory predicts that these species should be monomorphic for colour pattern (Fisher, 1930; Ford, 1964). The reason is that predators encounter abundant forms more frequently than rare forms. As a consequence, a greater proportion of the predator's population would have experienced the common form and thus individuals with that form would gain more protection from predation. Any mutation that alters the colour pattern would be removed by purifying frequency-dependant selection because predators would not recognize the rare mutant individuals as inedible (Greenwood *et al.*, 1981). Selection for monomorphism acts across the species boundaries as well as within them; the aposematic species in a Müllerian mimicry complex are expected to converge on a single colour form so as to share the cost of learning of naïve predators (Matthews, 1977). Edible prey species, on the contrary, are expected to be polymorphic so as to benefit from predators unfamiliarity; novel

forms will suffer less predation than common forms because predators would not recognize them as edible and thus would not target them specifically (Turner, 1984).

Most aposematic, mimetic species are monomorphic, as predicted by theory (Ackery and Vane-Wright, 1984); however, some Müllerian mimics show colour polymorphism. Among the classic cases of this phenomenon are the mimicry rings that include *D. chrysippus*, *Acraea encedon* and *A. encedana* in Africa (Owen *et al.*, 1994) and *Heliconius numata* in the Amazonian Basin (Brown and Benson, 1974). In theory, multiple mechanisms can modify the frequency-dependant selection by predators in such a way that a state of colour polymorphism is maintained. For example, different colour forms may co-exist sympatrically in the hybrid zones between geographical races (Mallet, 1993). Moreover, if the aposematic form is so heavily loaded by batesian mimics to the extent that predators encounter the mimic more frequently than the model, then predators will learn to target the aposematic form rather than avoiding it and both mimics and models will lose the protection provided by aposematism and mimetic resemblance, respectively (Malcolm, 1990). Moreover, it has been suggested that even in Müllerian mimicry, if member species are sufficiently variable in the degree of inedibility then the stronger (i. e. the more aposematic members) suffers from the presence of the weaker (i.e. the less aposematic members) in the same way they both suffer from the presence of genuine Batesian mimics. Such Quasi-Batesian mimetic association permits the evolution of colour diversity among superficially Müllerian mimicry complexes (Huheey, 1976; 1988).

The African monarch *Danaus chrysippus* is a cosmopolitan butterfly that is widely distributed across the tropics and subtropics of Africa and is considered as the most abundant butterfly in the continent. *D. chrysippus* prefers open country habitats and currently it reaches highest densities in areas affected by human disturbance such as farms and gardens (Owen, 1970; Smith and Owen, 1997). It is an aposematic butterfly that is both chemically defended and warningly coloured (Rothschild *et al.*, 1975; Brower *et al.*, 1975, 1978). The species is involved in a Müllerian mimicry ring that also includes the two sibling species *Acraea encedon* and *A. encedana* (Owen and Smith, 1993; Owen *et al.*, 1994). This mimicry complex is exploited by several Batesian mimics, the most important of which is the female diadem butterfly *Hypolimnas misippus* (Smith, 1976). *D. chrysippus* has multiple colour patterns that are vicariant across most of its geographic range, both inside and outside Africa; however, within the region of East and Central Africa, the species shows considerable colour polymorphism, with multiple forms occurring sympatrically and interbreeding extensively to produce many hybrid forms (Owen and Chanter, 1968; Smith, 1975a; Smith *et al.*, 1993). Within the polymorphism zone of *D. chrysippus* there are four major colour forms: *chrysippus*, *alcippus*, *dorippus* and *albinus* (Smith, 1980). Interestingly, the Müllerian mimics of *D. chrysippus* (i. e. *Acraea encedon* and *A. encedana*) also show the anomalous colour polymorphism (Owen *et al.*, 1994). This co-occurrence of a rare phenomenon in three sympatric, mimetic butterflies indicates that aposematic polymorphism in these species may have evolved following a common evolutionary pathway (Hassan and Idris, 2013).

In this review paper we address the theories on the origin and maintenance of aposematic polymorphism in *D. chrysippus*. The central argument of the paper is that each individual theory on this phenomenon has its limitations. These limitations could only be overcome through adopting a pluralistic theoretical approach that considers the full complexity of the ecology of *D. chrysippus*, including the evolutionary history of the species, the effects of mimicry (both Batesian and Müllerian) as well as the female-biased sex ratios caused by the male killing *Spiroplasma* bacterium.

## RESULTS

### *The 'hybrid zone' hypothesis*

For aposematic species that are divided into geographic races or vicariant subspecies/incipient species, hybridization takes place within the contact zones where intermediate forms are frequently observed (Mallet, 1993). According to the 'hybrid zone' hypothesis, the entire region of East and Central Africa represents a hybrid zone of *D. chrysippus* that connects regions in Africa where the species is monomorphic for different colour forms (i.e. f. *alcippus* in the west, f. *dorippus* in the north-east and f. *chrysippus* in the remaining areas). The theory states that the colour forms of *D. chrysippus* are not morphs of a polymorphic species but represent incipient species that arised through past geographic isolation by forest barriers during the Pleistocene epoch; when the environment changed during the mid-Holocene from forest to savannah habitats, *D. chrysippus* butterflies dispersed crossing the declining forest barriers. As a consequence, the contact has been restored between the incipient species and a giant hybrid zone was formed in the region where the floral change took place (which covers most of East and Central Africa). The extensive anthropic activities during the past two centuries (especially forest clearance and agriculture) further expanded the dispersal zone of *D. chrysippus* in Africa by providing more favourable habitats for the species (Smith, 1980; Smith *et al.*, 1993; 1998; 2010 Lushai *et al.*, 2003; 2005).

According to this hypothesis, partial reproductive isolation has evolved in *D. chrysippus* in the form of assortative mating between the incipient species (Smith, 1980; Smith *et al.*, 1998). This reproductive isolation was caused by the geographic isolation during the Pleistocene. Later, the invasion of *D. chrysippus* by the male-killing *Spiroplasma* bacterium has resulted in female-biased sex ratios throughout the hybrid zone. The hypothesis assumes that the species complex of *D. chrysippus* responds differently to the *Spiroplasma*, with certain forms being more resistant and thus showing lower *Spiroplasma* prevalences than other forms. If this is the case, then the colour forms will vary in the sex ratio with the resistant forms containing more males than the susceptible forms. It has been hypothesized that the variable abundance of males between the different forms of *D. chrysippus* is the underlying cause that restored the gene flow between colour forms/incipient species despite the behavioural barriers; females of the susceptible forms are forced to accept hybrid mating with males of the resistant forms because of the lack of males carrying their own colour form (Smith *et al.*, 1997; 2010; Lushai *et al.*, 2003; 2005; Hassan and Idris, 2013). When the sex ratio is highly biased toward females, hybrid mating may be selectively favoured as a reproductive strategy, even if it results in less fit progeny, because females adopting the alternative strategy (i.e. assortative mating) would frequently fail to find a mate, thus leaving no progeny at all.

There are multiple lines of evidence supporting the 'hybrid zone' hypothesis. First, the colour forms of *D. chrysippus* produce intermediate forms when hybridize (Smith, 1975a; 1980; Smith *et al.*, 1998). Intermediate coloration rarely results from mating between different mimetic forms because the resulting individuals will not resemble either of the two protected forms and thus would be subjected to higher predation rate. However, if the colour forms are, in fact, incipient species, then the non-adaptive production of intermediate forms is to be predicted in the hybrid zone. In addition, partial assortative mating has been observed between the colour forms of *D. chrysippus* (Smith, 1980; 1984; Gordon, 1984) Moreover, the geographic distribution of colour forms largely agrees with the theory, as it shows the predicted

morph ratio clines throughout Africa (Smith *et al.*, 1997). Finally, there are considerable field and experimental data suggesting that the susceptibility to the male-killing *Spiroplasma* varies with the colour pattern (Herren *et al.*, 2007); for example, f. *chrysippus* was observed to have higher susceptibility to male-killing than f. *dorippus*, with the former showing female-biased sex ratios while the later showing equal or near-equal sex ratio (Smith, 1975b).

#### **The 'mimetic load' hypothesis**

As we noted earlier, the model should be far more abundant than its mimic for Batesian mimicry to remain adaptive. If predators encounter the edible mimic more frequently than the aposematic model, most predators will learn to target individuals with that colour form; in other words, the aposematic signal will attract predators rather than deterring them (Malcolm, 1990). This effect has been hypothesized to take place in *D. chrysippus*; according to the 'mimetic load hypothesis' polymorphism has evolved in this species as a response to the negative frequency-dependant selection imposed by Batesian mimicry. Since abundant aposematic forms provide more protection than rare forms, they are consequently parasitized by more Batesian mimics; this, in turn, reduces the protection provided by the aposematic signal through the evolutionary time. On the contrary, the rare, less protected forms do not attract large mimetic populations thus avoiding dilution in the strength of their aposematic signal (Owen, 1970; Gordon 1987; Smith *et al.*, 1993). Theoretical modelling (Gavrilets and Hastings, 1998) suggests that this effect could counteract the aposematic selection for monomorphism if interspecific selection (i.e. the benefit of mimicry to the mimic and cost of mimicry to the model) are more intense than intraspecific selection (i.e. aposematism and palatability).

The mimetic complex of *D. chrysippus*, *Acraea encedon* and *A. encedana* is exploited by a wide variety of Batesian mimics including some of the female-limited forms of *Papilio dardanus* (Papilionidae), two forms of *Pseudacraea poggei* (Nymphalidae: Nymphalinae), *Mimacraea marshalli* (Lycaenidae), *Euryphene iris* (Nymphalidae: Satyrinae) and, most evidently, the female diadem butterfly *Hypolimnas misippus* (Nymphalidae), which has four different colour forms that show impressive resemblance to the four colour forms of *D. chrysippus* (Smith 1976; Gordon 1987). Supporting the 'mimetic load' hypothesis, the extent of colour polymorphism and Batesian mimicry show clear geographic association; in East and Central Africa, where the characteristic coloration of *D. chrysippus* is heavily exploited by Batesian mimics, polymorphism prevails, while in West Africa, where the species is mimicked only by the form *alcippoides* of female *H. misippus*, monomorphism dominates (Edmunds, 1969; Gordon 1987).

It is also possible that certain selective pressures acting within the Müllerian mimicry complex may have also contributed to maintenance of mimetic polymorphism. As is mentioned earlier, Müllerian mimics may vary in the degree of inedibility, and thus the less edible ones will suffer from the presence of the more edible (Huheey, 1976). Indeed, *D. chrysippus* show considerable geographic variation in aposematism throughout Africa (measured by the concentration of active cardiac glycosides in their tissues) with Western populations showing lower cardenolide concentration than that of Eastern populations (e. g. Rothschild *et al.*, 1975). Likewise, it is reasonable to speculate that inedibility may vary geographically in the sibling *Acraea* species. If this is the case, then it is possible that, in some regions in Africa, *D. chrysippus* is loaded by the less aposematic *Acraea* mimics, while in other regions the *Acraeas* are loaded by the less aposematic *D. chrysippus* mimics; only in regions where the three species have exactly the same degree of inedibility then the

conventional Müllerian selection for monomorphism takes place. To our knowledge, the possibility that the mimetic association between the three species in East and Central Africa represents a Quasi-Batesian rather than a Müllerian complex has not been systematically investigated by previous research.

#### ***The ‘cyclic extinctions’ hypothesis***

The invasion by an efficient male-killing endosymbiont has the potential to exert a substantial influence on the host population dynamics. This is because the spread of the male-killer will result in an increasingly female-biased sex ratio, and, consequently, to a state of male shortage. If the male-killer reaches extremely high prevalences, then host populations may undergo frequent extinctions due to the severe lack of males. The habitat patches that were emptied following extinction of heavily-infected populations will be colonized later by accidental dispersal from surrounding populations. As a result, the infection of individuals of a given species by an efficient male-killer may be manifested in the level of the species populations in the form of enhanced metapopulation dynamics (i. e. enhanced rate of extinctions and recolonizations of individual populations) (Heuch, 1978).

In a Müllerian mimicry complex, the interspecific frequency-dependant selection favouring the most abundant form *in the complex as a whole* will result in a gradual increase in the frequency of that favoured form *in the populations of each individual species within the complex*. This homogenizing effect could produce colour monomorphism given that one condition is met; that the populations remain demographically stable for sufficient time for selection to complete. This condition is unlikely to be met in the mimicry complex of *D. chrysippus* because the other two members *Acraea encedon* and *A. encedana* are infected by high prevalent male-killing *Wolbachia*; over 95% of females were found to carry the male-killer in some wild populations in Uganda and the population sex ratios were extremely biased (Jiggins *et al.*, 2000a; 2002). Moreover, the temporal analysis of *Wolbachia* prevalences in the two *Acraea* species has recorded recurrent prevalence fluctuations that are consistent with the occurrence of recurrent episodes of extinction for heavily-infected populations followed by recolonization by initially less-infected migrant populations (Hassan *et al.*, 2012a; in prep.).

Overall, these two lines of evidence (that *Wolbachia* prevalences are extremely high and that they show cyclic fluctuations over time) both suggest that the direction and intensity of Müllerian selection imposed on *D. chrysippus* by *Acraea* species fluctuates randomly over time following the extinction-recolonization episodes undergone by the later. The reason is that, with every extinction-recolonization episode, the original morph ratio of the population -the one that was shaped by previous Müllerian selection to match that of the other species- will be destroyed and replaced by a new morph ratio that have never been selected before to match that of the other species in the mimicry complex. Indeed, since the new morph ratio represents the migrant population rather than the original population, it follows that the morph ratio change is essentially random, reflecting only the chance event of habitat colonization. As a consequence, the cyclic extinctions that occur in the mimetic populations of *A. encedon* and *A. encedana* would repeatedly change the direction of Müllerian selection on the sympatric *D. chrysippus* population. The result would be highly variable selective pressures on *D. chrysippus* that favour multiple colour forms, which is a recipe for colour polymorphism (Hassan and Idris, 2013; Idris and Hassan, 2013).

According to this hypothesis, the root of aposematic polymorphism in *D. chrysippus* lies not in the species itself but, rather, in its Müllerian mimics; both

*Acraea* species are known to form discrete populations that vary extensively in colour form frequencies (Owen and Smith, 1993; Owen *et al.*, 1994). The spatial heterogeneity in the morph ratio is a necessary condition for extinction-recolonization cycles to affect the morph ratio in the way described by this hypothesis (Hassan and Idris, 2013; Idris and Hassan, 2013). If, alternatively, individuals of the species disperse widely without forming distinct populations, such as the case in *D. chrysippus* (Owen *et al.*, 1994), then the extinction of a local population and its replacement by migrants from a surrounding population would hardly affect the morph ratio at the habitat patch, because morph ratios are homogenous over large spatial scales. Moreover, although *D. chrysippus* is infected by the male-killing *Spiroplasma* (Jiggins *et al.*, 2000b) both the wild prevalences and the population dynamics of the *Spiroplasma* do not support the possibility of the existence of recurrent population extinctions in this species (Hassan *et al.*, 2012b). To conclude, although the colour polymorphism in *D. chrysippus* may not be affected by the male-killing *Spiroplasma*, it may nevertheless be maintained, at least in part, by the highly variable Müllerian selection imposed on the species because of the demographic effect of the male-killing *Wolbachia* on *A. encedon* and *A. encedana*.

## DISCUSSION

The paradox of aposematic polymorphism in *D. chrysippus* could be divided into two distinct questions: first, how polymorphism was evolved in the species? And second, how polymorphism was maintained in the species? The first question is about reconstructing the exact historical scenario by which the different colour forms of *D. chrysippus* have arisen from a single, ancestral colour form; theoretically speaking, purifying selection induced by predation is expected to eliminate any novel form shortly after invading the population through mutation or migration and before it reaches a significant level of abundance. The second question is about understanding the forces that maintained polymorphism within the species populations through the evolutionary time. It can be argued that, even if the novel colour forms have somehow managed to co-exist with the original form, achieving considerable abundance; it remains highly unlikely that they have exactly equal frequencies, thus, no matter how slight the initial differences in abundance are; positive frequency-dependant selection will automatically favour the colour form that happens to be initially more abundant resulting in an ever increasing magnitude of frequency variability between the colour forms and, consequently, to ever increasing intensity of selection for colour monomorphism.

The ecology of *D. chrysippus* provides us with two independent clues that represent intuitive starting points for any attempt to understand the aposematic polymorphism in this species: first, the geographic distribution of *D. chrysippus* suggests a tight correlation between two seemingly-unrelated phenomena that are, polymorphism and male killing. Outside East/Central Africa neither polymorphism nor male-killing occurs while within this region both phenomena have been observed (Owen and Chanter, 1968; Smith *et al.* 1997, 1998; Lushai *et al.*, 2003). Furthermore, the association between polymorphism and male-killing is replicated in the Müllerian mimics of *D. chrysippus* in Africa (i. e. *A. encedon* and *A. encedana*) (Owen and Smith, 1993; Owen *et al.*, 1994; Jiggins *et al.*, 1998; 2000a; Hassan and Idris, 2013). The co-occurrence of two rare phenomena in three mimetic species within a limited geographic zone is unlikely to be a pure coincidence; rather, it suggests that a subtle link might exist between these two superficially-independent phenomena (Majerus,

2003). The second clue is that *D. chrysippus* in Africa is influenced by a complex mimetic environment that shows high spatial and temporal variability; the species is involved in both Müllerian and Batesian mimetic associations that include multiple species such as *A. encedon*, *A. encedana* and *Hypolimnas misippus* (Smith, 1976; Owen and Smith, 1993; Owen *et al.*, 1994). Since aposematism and mimicry are both anti-predator adaptations that are intricately related (Joron and Mallet, 1998), it seems likely that the unusual aspect of aposematism (i. e. the colour polymorphism) might be linked to the unusual aspect of mimicry in *D. chrysippus* (i. e. the extensive and variable mimetic interactions).

Strictly speaking, the three hypotheses on the polymorphism in *D. chrysippus* are not “alternatives” of each other; this is because each hypothesis targets a distinct problem and exploits a distinct clue that is not identical to the problem/clue sets of other hypotheses. The ‘hybrid zone’ hypothesis is composed of two components; the first is about the origin of the multiple colour forms in *D. chrysippus*. This hypothesis avoids the difficulty posed by the purifying selection against rare forms by stating that colour forms were not produced in sympatry; alternatively, the colour forms are hypothesized to arise allopatrically from geographic isolation. Under this assumption, there will be no problem of the maintenance of polymorphism because there will be no ‘polymorphism’ in the first place; these colour forms are not morphs of a polymorphic species but incipient species in a species complex. However, this solution leads to another problem, namely, why those incipient species behave as if they are morphs of a single species? That is, by interbreeding freely and producing viable progeny throughout the hybrid zone. To account for this difficulty, a second component has been incorporated into the hypothesis, in which the first clue (the male-killing/polymorphism association) was exploited. The invasion by the male-killing *Spiroplasma* and the subsequent female-biased sex ratios were envisaged to force the hybrid mating between the semi-isolated incipient species of *D. chrysippus* complex.

The idea that colour diversity evolved through geographic separation is both theoretically attractive and well supported by geographic distribution data (e.g. Smith *et al.*, 1997), however, the proposition that these colour forms are incipient species that co-occur in a hybrid zone is much more disputable and is supported only by fragmentary and indirect evidence. We know of no other case in which there is a hybrid zone as large as East and Central Africa, comparable in size to that of the monomorphism zones themselves. Since reproduction between the different forms takes place normally throughout the huge contact zone and taking into consideration that there are no records of full reproductive isolation in the wild, it seems natural, then, to conclude that the possibility that *D. chrysippus* is a single, polymorphic species is more likely than the alternative possibility of *D. chrysippus* being a species complex. Moreover, there is no evidence to support the claim that hybrid mating occurs specifically as a response to male scarcity; on the contrary, the population sex ratios of *D. chrysippus* in the hybrid zone vary extensively from regions such as Uganda, where considerable female-bias was observed, to regions such as Sudan, where equal sex ratio was observed (Jiggins *et al.*, 2000b; Hassan *et al.*, 2012b). Despite this, the hybrid mating between different colour forms proceeds normally throughout the entire zone of East and Central Africa regardless to the status of the sex ratio. Finally, if sex ratio bias truly interferes with the pre-zygotic reproductive isolation during speciation then how the recent split of the sibling species *A. encedon* and *A. encedana* continued successfully without being interrupted by hybrid mating,

despite the infection of both species with the male-killing *Wolbachia* at much higher prevalences than that of *Spiroplasma* in *D. chrysippus*? (Jiggins *et al.*, 2002).

The ‘mimetic load’ hypothesis exploits the second clue, namely, the complex mimetic community of *D. chrysippus* in Africa but ignores the first clue, which is the geographic association with the phenomenon of male-killing. It is mainly a theory on the maintenance rather than the origin of colour polymorphism. This is because it is extremely difficult to see how a single or a few individuals carrying a novel colour form could gain a survival advantage from their deviation from the protective aposematic form. The difficulty stems from the fact that no predator would have ever encountered a similar prey and therefore no learned avoidance could be expected. On the other side, if the novel form, while still a minority, has reached a significant frequency in the population, then it can combine the protective advantages of the aposematic coloration and the reduced mimetic load.

Although the mimetic load could, in theory, select for polymorphism in the model species, in order for this effect to take place in the case of *D. chrysippus*, the cost of interspecific Batesian resemblance should exceed the benefits of both interspecific Müllerian resemblance and intraspecific aposematic resemblance (Gavrilets and Hastings, 1998). This may indeed be true for other aposematic mimetic species; however, it is somehow doubtful that the mimetic load is a major factor affecting the learned behaviour of *D. chrysippus* predators, and, consequently, the intensity of selection on the colour pattern. There are two independent reasons that make this unlikely: first, *D. chrysippus* is an extremely abundant species that outnumbers both its Müllerian and Batesian mimics (Owen, 1970; Smith and Owen, 1997). As a consequence, *D. chrysippus* individuals contribute to the learning of predators more than any other species in their mimicry complex; it follows, then, that intraspecific selection (i.e. aposematism) should be more powerful than interspecific selection (i. e. mimicry) in shaping the species coloration. The second reason is that the geographic distribution of the mimetic forms in Africa does not precisely coincide with that of their model forms; for example, in West Africa only one form of the model species occurs (*alcippus* form of *D. chrysippus*), but all the four forms of female *H. misippus* are found, thus three of them are effectively non-mimetic in this area. Even more paradoxical is that the one mimetic form (*alcippoides*) is relatively rare (Clarke *et al.*, 1995). These findings cast doubt on the presumed selective importance of Batesian mimicry in the maintenance of colour polymorphism in *D. chrysippus*.

The ‘cyclic extinctions’ hypothesis targets only one of the two puzzling questions regarding polymorphism in *D. chrysippus*, that is, the question of the maintenance rather than that of the origin. The existence of multiple colour forms with considerable initial frequencies is an assumption of this hypothesis rather than a conclusion. Given that the morph ratios have an initial spatial heterogeneity, the hypothesis proceeds to explain how this initial state can be maintained indefinitely against the direction of intraspecific aposematic selection. This is achieved through the recurrent random fluctuations in the direction of interspecific Müllerian selection caused by the male-killer-induced population extinctions. Thus, this hypothesis is the only one that exploits the two clues provided by the ecology of *D. chrysippus* (i.e. mimicry and male-killing).

Once again, this hypothesis does not provide a fully satisfying explanation for the exceptional case of *D. chrysippus*. The major criticism to this hypothesis is based on the earlier notion regarding the relative abundance of the species compared to its mimics. Due to the high dispersal potential and the absence of discrete populations in

*D. chrysippus* (Owen *et al.*, 1994), it is expected that any initial spatial heterogeneity in the morph ratio should be effectively eliminated, thus leading to a state of monomorphism prevailing over large distances. Since *D. chrysippus* is both more abundant and more widely dispersed than the two *Acraeas*, then, contrary to hypothesis, it is to be expected that the Müllerian selection imposed by *D. chrysippus* on the *Acraeas* (which is spatially homogenous and promotes monomorphism) is more intense than the selection imposed by the *Acraeas* on *D. chrysippus* (which is spatially heterogeneous and promotes polymorphism). According to this argument, *D. chrysippus* should be driving the two *Acraea* species toward monomorphism rather than the reversed situation of *D. chrysippus* being driven to polymorphism by the *Acraeas* (Gordon, 2013; Smith, 2013).

As the above discussion briefly shows, no current hypothesis on the colour polymorphism in *D. chrysippus* is perfectly compatible with field observations and the general predictions of the evolutionary theory. In our view, this necessitates the synthesis of a pluralistic approach towards this problem that combines the basic scenarios of the three hypotheses. Notably, none of these hypotheses actually contradicts the others as they are all mutually compatible. Moreover, each hypothesis has a distinct rather than an alternative scope to that of the other hypotheses, since all of them have their unique problem/clue sets. The underlying theory for such an approach is that polymorphism in *D. chrysippus* did not result directly from Batesian mimicry, Müllerian mimicry or male-killing. Alternatively, the state of polymorphism has arisen from an interaction between specific aspects of the three systems; these aspects have happened to co-occur in East and Central Africa but they do not coincide elsewhere. This pluralistic hypothesis could be criticized as being inelegant and highly unlikely because it requires a coincidence that involves three independent aspects rather than a single one. As a consequence, the 'pluralistic hypothesis' may be justifiably described as having lower prior possibility than any of the individual theories that it combines. However, considering that colour polymorphism in *D. chrysippus* is unique among the 157 species of aposematic milkweed butterflies (Ackery and Vane-Wright, 1984), it seems that an unlikely theory is exactly what we should be looking for; otherwise polymorphism would have evolved repeatedly in several species wherever its simple ecological requirements are met (i.e. either extensive Batesian mimicry, past geographic isolation or sex ratio distortion).

## REFERENCES

- Ackery, P. R. and Vane-Wright, R. I. (1984). *Milkweed Butterflies*. British Museum (Natural History), London.
- Barnard, C. (2004). *Animal behaviour: mechanism, development, function and evolution*. Pearson Education.
- Brower, L. P., Edmunds, M. and Moffitt, C. M. (1975). Cardenolide content and palatability of a population of *Danaus chrysippus* butterflies from West Africa. *Journal of Entomology* 49: 183-196.
- Brower, L. P., Gibson, D. O., Moffitt, C. M. and Panchen, A. L. (1978). Cardenolide content of *Danaus chrysippus* from three areas of East Africa. *Biological Journal of the Linnean Society* 10: 251-273.
- Brown, K. S. and Benson, W. W. (1974). Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepidoptera: Nymphalidae). *Biotropica* 6: 205-228.

- Clarke, C. A., Clarke, F. M. M. and Gordon, I. J. (1995). Mimicry and other controversial topics in East African Lepidoptera. *East African Natural History* 84: 3-18.
- Edmunds, M. (1969). Polymorphism in the mimetic butterfly *Hypolimnas misippus* L. in Ghana. *Heredity* 24: 281.
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Ford, E. B. (1964). *Ecological Genetics*. Methuen, London.
- Gavrilets, S. and Hastings, A. (1998). Coevolutionary chase in two-species systems with applications to mimicry. *Journal of Theoretical Biology* 191: 415-427.
- Gordon, I. J. (1984). Polymorphism of the tropical butterfly, *Danaus chrysippus* L., in Africa. *Heredity* 53: 583-593.
- Gordon, I. J. (1987). Natural selection for rare and mimetic colour pattern combinations in wild populations of the diadem butterfly, *Hypolimnas misippus* L. *Biological Journal of the Linnean Society* 31: 1-23.
- Gordon, I. J. (2013). Male-killing and aposematic polymorphism in African butterflies: Is there a connection? *Ideas in Ecology and Evolution* 6: 20-21.
- Greenwood, J. J. D., Wood, E. M. and Batchelor, S. (1981). Apostatic selection of distasteful prey. *Heredity* 47: 27-34.
- Hassan, S. S. M., Idris, E. (2013). Male-killing in African butterflies. *Trends in Evolutionary Biology* 5: 7-14.
- Hassan, S. S. M., Idris, E. and Majerus, M. E. N. (2012a). Male-killer dynamics in the tropical butterfly, *Acraea encedana* (Lepidoptera: Nymphalidae). *Journal of Insect Science* DOI: (10.1111/j.1744-7917.2012.01570.x).
- Hassan, S. S. M., Idris, E. and Majerus, M. E. N. (2012b). Male-killer dynamics in *Danaus chrysippus* (L.) (Lepidoptera: Nymphalidae) in East Africa. *African Journal of Ecology* 50: 489-499.
- Herren, J. K., Gordon, I., Peter, W. H., Holland, P. W. H. and Smith, D. (2007). The butterfly *Danaus chrysippus* (Lepidoptera: Nymphalidae) in Kenya is variably infected with respect to genotype and body size by a maternally transmitted male-killing endosymbiont (*Spiroplasma*). *International Journal of Tropical Insect Science* 27: 62-69.
- Heuch, I. (1978). Maintenance of butterfly populations with all female broods under recurrent extinction and recolonization. *Journal of Theoretical Biology* 75: 115-122.
- Huheey, J. E. (1976). Studies of warning coloration and mimicry. VII. Evolutionary consequences of a Batesian-Müllerian spectrum: a model for Müllerian mimicry. *Evolution* 30: 86-93.
- Huheey, J. E. (1988). Mathematical models of mimicry. *American Naturalist* 131: 22-41.
- Idris, E. and Hassan, S. S. M. (2013). Biased sex ratios and aposematic polymorphism in African butterflies: A hypothesis. *Ideas in Ecology and Evolution*. 6: 5-16.
- Jiggins, F. M., Hurst, G. D. D. and Majerus, M. E. N. (1998). Sex ratio distortion in *Acraea encedon* (Lepidoptera: Nymphalidae) is caused by a male-killing bacterium. *Heredity* 81: 87-91.
- Jiggins, F. M., Hurst, G. D. D., Dolman, C. E. and Majerus, M. E. N. (2000a). High-prevalence male-killing *Wolbachia* in the butterfly *Acraea encedana*. *Journal of Evolutionary Biology* 13: 495-501.
- Jiggins, F. M., Randerson, J. P., Hurst, G. D. D. and Majerus, M. E. N. (2002). How can sex ratio distorters reach extreme prevalences? Male-killing *Wolbachia* are

- not suppressed and have near-perfect vertical transmission efficiencies in *Acraea encedon*. *Evolution* 56: 2290-2295.
- Jiggins, F., Hurst, G., Jiggins, C., Schulenburg, J. and Majerus, M. (2000b). The butterfly *Danaus chrysippus* is infected by a male-killing *Spiroplasma* bacterium. *Journal of Parasitology* 120: 439-446.
- Joron, M. and Mallet, J. (1998). Diversity in Mimicry: paradox or paradigm? *Trends in Evolutionary Biology* 13: 461-466.
- Lushai, G., Allen, J. A., Goulson, D., Maclean, N. and Smith, D. A. S. (2005). The butterfly *Danaus chrysippus* (L.) in East Africa comprises polyphyletic, sympatric lineages that are, despite behavioural isolation, driven to hybridization by female-biased sex ratios. *Biological Journal of the Linnean Society* 86: 117-131.
- Lushai, G., Smith, D. A. S., Gordon, I. J., Goulson, D., Allen, J. A. and Maclean, N. (2003). Incomplete sexual isolation in sympatry between subspecies of the butterfly *Danaus chrysippus* (L.) and the creation of a hybrid zone. *Heredity* 90: 236-246.
- Majerus, M. E. N. (2003). *Sex wars: Genes, Bacteria, and Biased Sex Ratios*. Princeton University Press. Princeton, New Jersey.
- Malcolm, S.B. (1990) Mimicry: status of a classical evolutionary paradigm. *Trends in Ecology and Evolution* 5: 57-62.
- Mallet, J. (1993). Speciation, raiation, and colour pattern evolution in *Heliconius* butterflies: evidence from hybrid zones, in: *Hybrid Zones and the Evolutionary Process* (Harrison, R.G., ed.), pp. 226-260, Oxford University Press.
- Matthews, E. G. (1977). Signal-based frequency-dependent defense strategies and the evolution of mimicry. *American Naturalist* 111: 213-222.
- Owen, D. F. (1970). Mimetic polymorphism and the palatability spectrum. *Oikos* 21: 333-336.
- Owen, D. F. and Chanter, D. O. (1968). Population biology of tropical African butterflies. 2. Sex ratio and polymorphism in *Danaus chrysippus* L. *Revue Zoologiques et Botaniques Africaines* 78: 81-97.
- Owen, D. F. and Smith, D. A. S. (1993). *Danaus chrysippus* and its polymorphic Müllerian mimics in tropical Africa (Lepidoptera: Nymphalidae: Danainae). *Tropical Lepidoptera research* 4: 77-81.
- Owen, D. F., Smith, D. A. S., Gordon, I. J. and Owiny, A. M. (1994). Polymorphic Müllerian mimicry in a group of African butterflies: a reassessment of the relationship between *Danaus chrysippus*, *Acraea encedon* and *Acraea encedana* (Lepidoptera: Nymphalidae). *Journal of Zoology* 232: 93-108.
- Rothschild, M., Von Euw, J., Reichstein, J., Smith, D. A. S. and Pierre, J. (1975). Cardenolide storage in *Danaus chrysippus* (L.) with additional notes on *D. plexippus* (L.). *Proceedings of the Royal Society B* 190: 1-31.
- Smith, D. A. S. (1975a). Genetics of some polymorphic forms of the African butterfly *Danaus chrysippus* L. (Lepidoptera: Danaidae). *Entomologica Scandinavica* 6: 134-144.
- Smith, D. A. S. (1975b). All-female broods in *Danaus chrysippus* L. and their ecological significance. *Heredity* 34: 363-371.
- Smith, D. A. S. (1976). Phenotypic diversity, mimicry and natural selection in the African butterfly *Hypolimnas misippus*. *Biological Journal of the Linnean Society* 8: 183-204.

- Smith, D. A. S. (1980). Heterosis, epistasis and linkage disequilibrium in a wild population of the polymorphic butterfly *Danaus chrysippus*. *Zoological Journal of the Linnean Society* 69: 87-109.
- Smith D. A. S. (1984). Mate selection in butterflies: competition, coyness, choice and chauvinism. In: Vane-Wright RI, Ackery PR (eds). *The Biology of Butterflies. Symposia of the Royal Entomological Society of London 11*. Academic Press: London. pp 225-244.
- Smith, D. A. S. (2013). On refining hypotheses for biased sex ratios and aposematic polymorphism in African butterflies: a commentary. *Ideas in Ecology and Evolution* 6: 17-19.
- Smith, D. A. S. and Owen, D. F. (1997). Colour genes as markers for migratory activity: The butterfly *Danaus chrysippus* in Africa. *Oikos* 78: 127-135.
- Smith, D. A. S., Gordon, I. J. and Allen, J. A. (2010). Reinforcement in hybrids among once isolated semispecies of *Danaus chrysippus* (L.) and evidence for sex chromosome evolution. *Ecological Entomology* 35: 77-89.
- Smith, D. A. S., Gordon, I. J., Depew, L. A. and Owen, D. F. (1998). Genetics of the butterfly *Danaus chrysippus* L. in a broad hybrid zone, with special reference to sex ratio, polymorphism and intragenomic conflict. *Biological of Journal Linnean Society* 65: 1-40.
- Smith, D. A. S., Owen, D. F., Gordon, I. J. and Lowis, N. K. (1997). The butterfly *Danaus chrysippus* (L.) in East Africa: polymorphism and morph-ratio clines within a complex, extensive and dynamic hybrid zone. *Zoological Journal of the Linnean Society* 120: 51-78.
- Smith, D. A. S., Owen, D. F., Gordon, I. J. and Owiny, A. M. (1993). Polymorphism and evolution in the butterfly *Danaus chrysippus* (L.) (Lepidoptera: Danainae). *Heredity* 71: 242-251.
- Turner, J. R. G. (1984). Mimicry: the palatability spectrum and its consequences, in *The Biology of Butterflies* (Vane-Wright, R.I. and Ackery, P.R., eds), pp. 141–161, Academic Press.