Commentary

On refining hypotheses for biased sex ratios and aposematic polymorphism in African butterflies: a commentary

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Idris and Hassan (2013) are surely right to emphasize that aposematic species and especially those involved in Müllerian mimicry complexes are expected to be (and usually are) monomorphic. Thus, the three species under discussion, *Danaus chrysippus*, *Acraea encedon* and *A. encedana* are paradoxical because they are in many populations (though by no means all) polymorphic. In fact, *D. chrysippus* is monomorphic through most of its vast range, even in Africa, and invariably so in Asia and Australia; the authors do not acknowledge this. It is the restriction of *D. chrysippus* polymorphism in East Africa that is especially paradoxical. *Acraea encedon* is monomorphic in extreme West Africa (Senegal & Gambia) and *A. encedana* is monomorphic throughout West Africa.

Some predators are able to generalize over several different prey types that may be adjudged polymorphic to the human eye (Duncan & Sheppard 1965) and there are many examples of ‘jack of all trades’ mimicry, especially among syrphid flies and their hymenopteran models (Edmunds 2000; Penney et al. 2012). It is wise to acknowledge that the eyes of humans and butterfly predators, especially birds, differ profoundly and that non-visual attributes such as flight behaviour and olfactory cues are also used by predators.

The manipulative influence of early male-killing endosymbionts on their hosts is correctly described by the authors. In particular, infected females should have a fitness advantage over uninfected ones through reduced sibling competition for resources and the opportunity to cannibalize male eggs, as occurs routinely in ladybird beetles (Majerus, 1994). The high efficiency of its matrilineal vertical transmission is the other factor integral to the success of the endosymbiont. In batch

layers such as the two *Acraeas*, the proximity of eggs facilitates cannibalism of their dead brothers by females but whether it could occur on a regular basis in *D. chrysippus* is more problematical as this butterfly has always been thought to scatter its eggs widely, and even to be deterred from laying eggs on a leaf already occupied by an egg or caterpillar. However, Smith (2013)—in fairness, a publication that Idris and Hassan cannot have seen—shows that, if presented with a choice between host plants growing in patches or as isolates, *D. chrysippus* much prefers the latter. The overloading of isolated plants with eggs is a scenario in which the benefits of male-killing may be realized. There is one caveat: the *D. chrysippus* population investigated by Ileri, Gordon and Smith (in prep.) is heavily parasitized by *Spiroplasma*; we do not know if uninfected females oviposit in similar fashion. In other words, it is possible that *Spiroplasma* manipulates the behaviour of its host to its own advantage.

I believe Idris and Hassan are right to dismiss the ‘mimetic overload’ hypothesis of Owen (1971) as an explanation of co-mimetic polymorphism; it does not fit the facts, especially as the geographical match of analogous morphs is so imperfect. However, in altogether dismissing Batesian mimicry in the paradoxical case of *Hypolimnas misippus* and *D. chrysippus*, Gordon et al. (2010) would disagree with Idris and Hassan; the former authors claim to show for the first time that Batesian mimicry functions intermittently but that other factors such as sexual, apostatic, and *r/K* selection are also relevant to interpreting the polymorphism. The recurring mistake in the long debate on the *misippus/chrysippus* relationship has been the assumption that Batesian or Müllerian mimicry must be either the whole story or

totally invalid. I acknowledge Idris and Hassan's claim that the mimicry at Khartoum, as in so many other places, appears problematical.

I think the authors are mistaken to dismiss the 'hybrid zone' hypothesis to account for polymorphism in *D. chrysippus*, for which there is much supporting evidence (Smith et al. 1997, 1998, Smith 2013). Although the hypothesis does not work for the *Acraeas*, *D. chrysippus* is a very different butterfly. The ecologies of *D. chrysippus* and the two *Acraeas* differ profoundly in several respects: in particular, the former is highly dispersive, migratory over long distances and polyphagous, whereas both *Acraeas* are monophagous and form tight colonies around their host plants from which females alone disperse short distances to found new colonies. There is no good reason to expect that one explanation for the evolution of their polymorphisms should apply to all three species. I profoundly disagree with the statement: 'Thus, in a habitat patch where the three species co-exist, a similar pattern of extinction-recolonisation cycles will occur in the three sympatric populations.' (Idris and Hassan 2013: 10). Wherever the three species have been studied in sympatry (Dar es Salaam, Nairobi and Kampala), the main difference is that 'morph' frequencies in *D. chrysippus* fluctuate seasonally as its component semispecies migrate into and out of the study area, whereas in the *Acraeas*, morph frequencies are relatively stable within any one colony. The difference is explained by the fact that *D. chrysippus* 'morphs' are in reality incipient species, whereas in the *Acraeas* they are mere colour variants of a single species.

Again, in positing alternating extinction-recolonisation events interspersed by long periods of demographic stability as a mechanism for maintaining polymorphism, I feel it could work for the *Acraeas* but not for *D. chrysippus* in which polymorphisms are stabilized across wide areas. Idris and Hassan should acknowledge that the two *Acraeas* differ fundamentally in their respective mimicries of *chrysippus*. On the one hand, *A. encedana* is a convincing mimic throughout its range (Pierre, 1976), the biogeography of its morphs matching those of *chrysippus* from west, through east and down to southern Africa. On the other hand, *A. encedon* is more often than not an unconvincing mimic, and where it is so in Tanzania (Owen & Smith, 1991), *encedana* is absent. The fundamental differences in polymorphism and mimicry between the two *Acraeas*, convincing Müllerian mimicry in *A. encedana* and feeble mimicry in *A. encedon*, argues against finding a single explanation for the origin of both.

With respect to the 'hybrid zone' hypothesis, Idris and Hassan (2013: 12) say 'a critical assumption of our hypothesis is that colour forms do not affect susceptibility to male killing, while a critical assumption of the 'hybrid zone' hypothesis is that colour forms

do indeed vary in susceptibility. Thus, a clear test for both hypotheses [the alternative being their own] would be to investigate the relationship between colour pattern and *Spiroplasma* infection in *D. chrysippus* through a large study conducted within substantial spatial and temporal scales.' Such a study was in fact carried out by Smith (1975b) at Dar es Salaam, many years before the discovery of *Spiroplasma*, in which it was shown that *D. c. dorippus* was substantially less susceptible to all-female brooding (subsequently proved to be caused by *Spiroplasma*) than *D. c. chrysippus*. Smith (1975b) proposed a model of which the prime feature was that *D. c. dorippus* carried a suppressor gene which enabled it to resist male-killing. An unpublished study under way at Nairobi (Ireru *et al.*, in prep.) will endorse the Dar es Salaam finding in establishing that *Spiroplasma* infection is high in *D. c. chrysippus* but low in *D. c. dorippus*; indeed, the new evidence implies that *Spiroplasma* infection is essentially a symbiosis largely with *D. c. chrysippus* and hybrid forms of which it is one of the parents.

References

- Duncan C.J., and P.M. Sheppard. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour* 24: 269–282. [CrossRef](#)
- Edmunds M. 2000. Why are there good and poor mimics? *Biological Journal of the Linnean Society* 70: 459–466. [CrossRef](#)
- Gordon I.J., Edmunds M., Edgar J.A., Lawrence J., and D.A.S. Smith. 2010. Linkage disequilibrium and natural selection for mimicry in the Batesian mimic *Hypolimnas misippus* (L.) in the Afrotropics. *Biological Journal of the Linnean Society* 100: 180–194. [CrossRef](#)
- Idris, E. and S.S.M. Hassan. 2013. Biased sex ratios and aposematic polymorphism in African butterflies: A hypothesis. *Ideas in Ecology and Evolution* 6: 5–16. [CrossRef](#)
- Majerus, M.E.N. 1994. *Ladybirds*. London: Collins.
- Owen, D.F. 1971. *Tropical Butterflies*. Oxford: Clarendon Press.
- Owen D.F. and D.A.A. Smith. 1991. All-female broods and mimetic polymorphism in *Acraea encedon* (L.) (Lepidoptera: Acraeidae) in Tanzania. *African Journal of Ecology* 29: 241–247. [CrossRef](#)
- Penney H.D., Hassall C., Skevington J.H., Abbott K.R., and T.N. Sherratt. 2012. A comparative analysis of the evolution of imperfect mimicry. *Nature* 483: 461–464. [CrossRef](#)
- Pierre J. 1976. Polymorphismes et mimétisme chez deux espèces jumelles, *Acraea encedon* et *A. encedana*. *Annales du Société Entomologique de France* 12: 621–638.

- Smith D.A.S. 1975. All-female broods in *Danaus chrysippus* L. and their ecological significance. *Heredity* 34: 363–371. [CrossRef](#)
- Smith D.A.S. 2013. African Queens and their Kin: a Neo-Darwinian Odyssey. Harpenden, UK: Brambleby Books Ltd.
- 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 Journal of the Linnean Society* 65: 1–40.
- Smith, D.A.S., Owen, D.F., Gordon, I.J. and Lewis, 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. [CrossRef](#)