



Review

Female-limited mimetic polymorphism: a review of theories and a critique of sexual selection as balancing selection

Krushnamegh Kunte*

Section of Integrative Biology, University of Texas, Austin, TX, U.S.A.

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Mimicry theory played a prominent role in the development of natural selection theory, and sparked a long-lasting interest in the observation that Batesian mimicry in some butterflies is female limited and polymorphic. Mimetic females of polymorphic species clearly have a selective advantage due to reduced predation pressure, but the selective forces that maintain nonmimetic female forms remain unclear. Attention has lately been focused on three explanations based on sexual selection: (1) male mate preference, (2) pseudo-sexual selection and (3) sexual harassment avoidance. These are thought to favour nonmimetic female forms and allow them to persist in the population via balancing selection. Here I review the assumptions and evidence for each of these hypotheses and assess their relative merit. I find that: (a) key predictions of the hypotheses have not been tested, (b) the hypotheses interpret surrogate measures of fitness trade-offs implicit in balancing selection (e.g. mating frequency) differently, and (c) sexual selection may not maintain nonmimetic females at high mimic frequencies if male mate preference is frequency dependent. As a result, none of the hypotheses is unequivocally supported by available data. I show that a fourth, non-sexual selectionist hypothesis, namely that physiological trade-offs maintain mimetic female polymorphism, is based on unclear assumptions and probably explains minor variation in female polymorphism. Finally, I show that the basic framework of frequency-dependent mimetic advantage, independent of sexual selection, can adequately explain female-limited mimetic polymorphism in a broad range of species. Testing this framework should be a priority in resolving this problem.

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Butterflies show a spectacular diversity of Batesian mimicry, in which palatable prey species ('mimics') derive protection from visually hunting predators by their resemblance to toxic or otherwise defended and usually strikingly patterned species ('models') (Bates 1862; Eltringham 1910; Cott 1940; Wickler 1968; Rettenmeyer 1970; Edmunds 1974; Ruxton et al. 2004). Perhaps the most intriguing type of Batesian mimicry is female-limited polymorphic mimicry, in which males are nonmimetic and monomorphic while females are polymorphic, showing one or more mimetic forms (Wallace 1865; Trimen 1869; Punnett 1915; Ford 1975). Males in such female-limited mimetic species invariably represent the ancestral wing colour pattern of the species, the mimetic female forms having diverged from their ancestral, male-like wing patterns (Kunte 2008). The female limitation of mimicry is usually explained by a combination of sex-dependent predation pressure and sexual selection: (1) female butterflies carry heavy egg-loads

and are therefore aerodynamically constrained in their escape flights. Thus, females are thought to be more vulnerable to predation and presumably gain a greater fitness advantage from Batesian mimicry compared to males (Wallace 1865; Chai & Srygley 1990; Srygley & Chai 1990; Marden & Chai 1991; Ohsaki 1995), and (2) wing colour patterns are assumed to be constrained by sexual selection to a much greater extent in males than in females. Thus, male mimicry is selectively disfavoured when its natural selective advantage is overwhelmed by the sexual selective advantage of nonmimetic coloration that may be more successful during inter- or intrasexual encounters (Belt 1874; Brower 1963; Turner 1978; Lederhouse & Scriber 1996). However, these hypotheses do not explain the presence of and natural variation in female-limited mimetic polymorphism. The general pattern of female-limited mimetic polymorphism is that species have a single male-like nonmimetic female form and one or more mimetic female forms that mimic models with completely different appearances (e.g. Asian *Papilio polytes* and *P. memnon*; see Fig. 1). In some mimics, all female forms are mimetic, with different forms mimicking different models (e.g. *Hypolimnas misippus* and *Euripus nyctelius*, and most populations of *Papilio dardanus*; see Fig. 1). In yet other species,

* Correspondence: K. Kunte, FAS Center for Systems Biology, Harvard University, 52 Oxford Street, Cambridge, MA 02138, U.S.A.

E-mail address: kkunte@cgr.harvard.edu

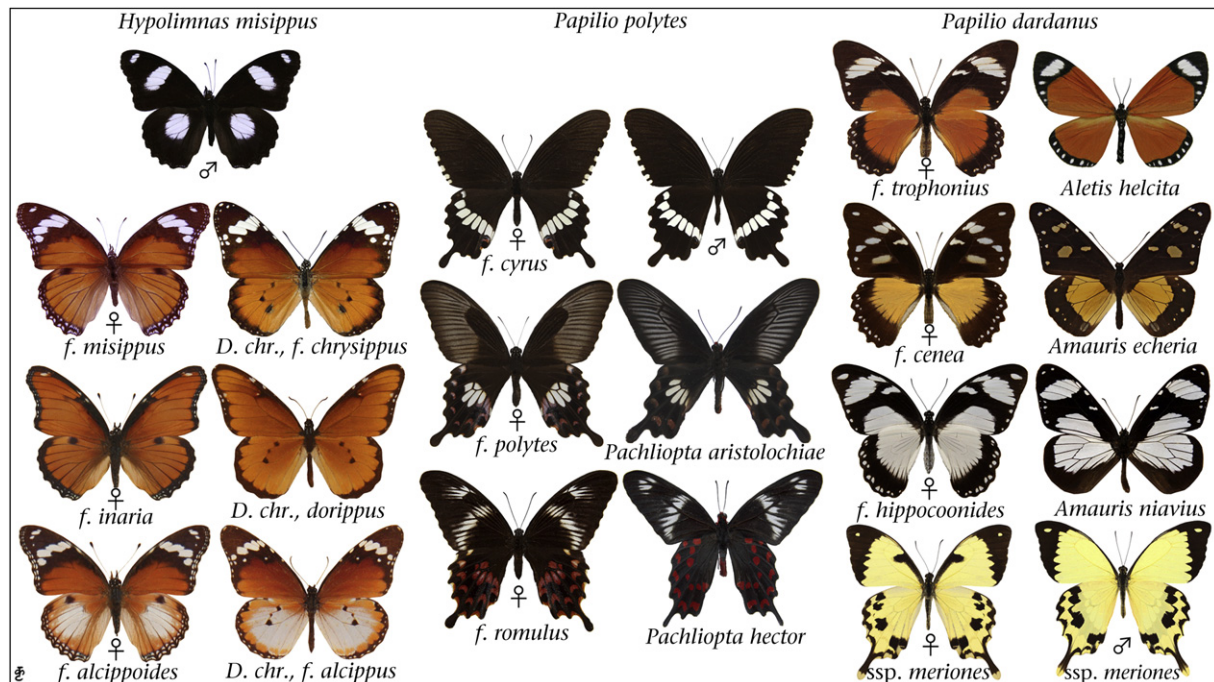


Figure 1. Three examples of female-limited polymorphism in Batesian mimicry. *Hypolimnias misippus*: across western India and Africa, males are monomorphic and nonmimetic whereas females are trimorphic, each mimicking a different form of the model, *Danaus chrysippus*. There are no male-like nonmimetic females in this species (Ford 1975; Smith 1984; Wynter-Blyth 1957). *Papilio polytes*: across their distributional range in the Oriental Region and in several subspecific variations, *P. polytes* males are monomorphic and nonmimetic whereas females may be polymorphic, with one male-like nonmimetic form and usually one but sometimes two form(s) mimicking locally abundant *Pachliopta* models. The subspecies *Papilio p. romulus* in Sri Lanka and peninsular India has trimorphic females, with a male-like form (*cyrus*) and two mimetic forms (*polytes*, also known as *stichius*, and *romulus*) (Ford 1975; Kunte 2000; Wallace 1865). *Papilio dardanus*: males of this African species are monomorphic and nonmimetic in several subspecific variations whereas females in most populations are polymorphic, mimicking *Danaus*, *Amauris*, *Acraea*, *Bematistes* and day-flying moth models. Only the subspecies in Madagascar (illustrated in the bottom row), Grande Comore Island and Abyssinia have male-like nonmimetic females (Eltringham 1910; Sheppard 1962; Trimen 1869). Photos: Krushnamegh Kunte.

there is a single mimetic female form and a single nonmimetic female form (e.g. *P. glaucus*) (Scriber et al. 1996). Attempts to explain this diversity have fostered continued interest in mimetic female polymorphism as a system to test theories of natural and sexual selection.

The genetic basis of female-limited mimetic polymorphism is fairly well known (reviewed in: Ford 1975; Sheppard 1975; Turner 1977, 1984; Charlesworth 1994; Mallet & Joron 1999). However, the phenomenon is still puzzling from the selection perspective because it is uncertain what selective pressures prevent the naturally selected mimetic female form(s) from completely replacing the nonmimetic female form(s) in most species. This is because the latter are readily taken by predators as prey, and are thus often natural selectively disadvantaged in comparison with the competing mimetic female forms. It is also unclear what prevents one mimetic form from replacing other mimetic forms. Five main hypotheses have been proposed to explain the maintenance of female-limited polymorphism in Batesian mimetic systems. Three of these invoke sexual selection as the principal driver of female polymorphism, and these have been more popular in the past few decades: (1) male mate preference (Burns 1966), (2) pseudo-sexual selection (Vane-Wright 1984) and (3) sexual harassment avoidance (Robertson 1985; Cordero 1992; Cook et al. 1994). The remaining two hypotheses emphasize the role of ecological interactions: (4) ecological–physiological trade-offs (Ohsaki 2005) and (5) the frequency-dependent advantage of mimicry (Sheppard 1962; Barrett 1976; Turner 1978). Each of these five hypotheses assumes that female-limited mimetic polymorphisms are maintained by balancing selection, which can be understood by elucidating the costs and benefits accruing to each female form under different social environments. Most of them assume either that the mimetic

female forms are favoured by natural selection, which may carry some balancing cost at higher relative frequencies, or that the nonmimetic female forms have some balancing selective advantage. I will later review these assumptions in detail.

Nonselectionist explanations for the persistence of nonmimetic female forms have also been proposed (e.g. overdominance: Ford 1965; gene flow: Prout 1967; Cook et al. 1994), which could persistently introduce ‘maladapted’ nonmimics in a population of naturally selected mimics. However, data on the genetics of mimicry and population structure are incompatible with these explanations (Ford 1975; Sheppard 1975), so I will not discuss them further. In this review I will assess the relative strengths and examine evidence for each of the five selectionist hypotheses. It will be shown that frequency-dependent advantage of mimicry is the most parsimonious explanation, which is also more likely to account for the greatest variation in mimetic polymorphism.

MALE MATE PREFERENCE

Burns (1966) hypothesized that in female-polymorphic butterflies, mimetic female forms are maintained by natural selection while nonmimetic female forms are maintained by male mate preference. Burns studied female polymorphism in the North American *P. glaucus*, in which the nonmimetic female form is male-like and the melanic form mimics *Battus philenor*. The mimetic advantage of the melanic form is well known (Brower 1957, 1958; Brower & Brower 1962; Ries & Mullen 2008). To test the male mate preference hypothesis, Burns counted the number of spermatophores found in females of each form. Spermatophores contain sperm and nutrients, which are passed on as a package to females during copulation. If a female mates multiple times, spermatophore

from the last mating is usually used first; traces of spermatophores persist for a long time; and the number of spermatophores is a good correlate of female mating frequency (Burns 1968; Sims 1979).

Burns (1966) found that wild-caught nonmimetic females of *P. glaucus* carried more spermatophores than did mimetic females. Older females usually carry more spermatophores (Lederhouse 1981), but differences in age did not account for differences in the mating frequency of the two female forms. From this, Burns concluded that males had preferentially mated with the nonmimetic females, and therefore the nonmimetic female form was probably maintained by male mate choice. Another study supported these conclusions (Lederhouse 1995), although two factors make these conclusions problematic. First, a single mating is sufficient to fertilize all the eggs laid by an average female, and multiple matings do not increase fecundity in *Papilio* (Levin 1973; Sims 1979; Lederhouse & Scriber 1987). Although multiple matings increase fertility and egg viability in old females (Lederhouse 1981; Lederhouse & Scriber 1987), old females of both *P. glaucus* forms were mated multiply. Second, results from more extensive studies contradicted Burns's findings: in numerous populations of *P. glaucus* with varying proportions of mimetic and nonmimetic females, there was no difference in the number of spermatophores carried by the two female forms (Makielski 1972; Pliske 1972; Levin 1973; Platt et al. 1984; Lederhouse & Scriber 1987). Thus, female dimorphism in *P. glaucus* remains largely unexplained, without supporting Burns's hypothesis.

A second set of studies investigated whether male mate preference maintains different mimetic forms in an African species, *Hypolimnas misippus* (Smith 1984). In this species, all female forms are mimetic, each mimicking a different form of the model, *Danaus chrysippus* (Fig. 1). It was shown that males preferentially courted and mated with one mimetic female form over others, although Smith acknowledged that sexual selection and natural selection were confounded since relative frequencies of models and the different mimetic forms fluctuated seasonally and across years. Unfortunately, temporal variation in male mate preference was not studied. Moreover, these studies were designed to test for male mate preference, not its role in maintaining mimetic female polymorphism.

Thus, available evidence from the only two systems studied so far does not support the hypothesis that males preferentially mate with a subset of female forms available, countering natural selection that favours other female forms. Unequivocal demonstration is therefore needed not just of the existence of male mate preference for a subset of female forms but also: (1) the relative mating advantage to male-preferred and natural selectively disfavoured female forms, (2) whether the mating advantage to male-preferred females balances the natural selective advantage of the other mimetic forms, and (3) that the two selective forces produce similar lifetime fecundity in the alternative female forms. Without a matching selective advantage, male mate preference cannot act as a balancing force against natural selection in maintaining female polymorphism.

PSEUDO-SEXUAL SELECTION

Vane-Wright (1984, pages 251–253) advanced the concept of pseudo-sexual selection, defining it as 'a process, whereby one sex shows a preference for a particular morph of the opposite sex due to initial misidentification with a potential competitor or synergist of its own sex'. This idea shares many elements with the male mate preference hypothesis in the specific case of mimetic butterflies, and can be simply explained as follows. The pseudo-sexual selection hypothesis starts with the same premise as the male mate preference hypothesis, that the mimetic females are favoured by

natural selection but the male-like nonmimetic females may be mated sooner or more frequently. The difference between the two hypotheses is the mechanism by which nonmimetic females gain a mating advantage. In the case of the male mate preference hypothesis, it is an innate male preference for a female of the ancestral male-like form. Pseudo-sexual selection argues for a more contrived mechanism. Most close-range communication and mate preference in butterflies is largely mediated through pheromones, when olfactory cues may overwhelm visual cues (Boppré 1984; Vane-Wright & Boppré 1993). However, male butterflies are highly visually oriented in social settings, vigorously interacting with other males and approaching any objects that may be suggestive of male wing colour patterns from a long distance (Silberglied 1984; Vane-Wright 1984). Hence, Vane-Wright speculated that at long range, males may visually mistake male-like females for other males and approach them to engage in either intrasexual combats or 'synergistic activities' such as mud-puddling; but at close range, they realize their mistake (perhaps through olfactory cues) and switch to courtship. Thus, the initial visual misidentification by males may predispose male-like females to be approached and courted more frequently, increasing their likelihood of insemination. Mimetic females, on the other hand, may be discovered, courted and inseminated less frequently.

This hypothesis assumes that the number of eggs laid by a female depends solely on the female's postmating life span, irrespective of the female's mimetic/nonmimetic form. Therefore, in order for pseudo-sexual selection to maintain balanced female polymorphism, male-like females should mate much sooner than mimetic females and have a longer postmating life span in which to lay eggs, but this advantage may be offset by their lower life expectancy (Vane-Wright 1984). Thus, the predicted pseudo-sexual selective advantage of early mating of the nonmimetic females counteracts the natural selective advantage of longer life span of the mimetic females.

This hypothesis has never been tested. I doubt, for two reasons, that it will be generally applicable, if indeed it explains any case of female-limited mimetic polymorphism. First, male approaches to females are probably frequency dependent (Makielski 1972; Levin 1973). For example, the frequency with which male *Papilio dardanus* approach and court female forms is determined by the relative frequency of the female forms in the population, and is not based on whether females are male-like (Cook et al. 1994; see Sexual Harassment Avoidance below for details). Second, and more importantly, available data show that virgin females are rarely encountered: both mimetic and nonmimetic female forms of *P. glaucus* as well as females of many other nonmimetic or mimetic species mate quickly after eclosion, perhaps within a few hours (Burns 1968; Makielski 1972; Pliske 1972; Sims 1979; Platt et al. 1984; Scriber et al. 1988/1989). Hence, the predicted delay in mating of mimetic females occurs rarely in nature, if at all, and is probably insufficient to offset the benefit of reduced predation on mimetic females.

SEXUAL HARASSMENT AVOIDANCE

The sexual harassment avoidance hypothesis is rooted in the well-known example of female polymorphism in *Ischnura* damselflies (Robertson 1985; Cordero 1992). In many species of *Ischnura*, females can either be cryptic ('gynomorph' females) or brightly coloured like males ('andromorph' females). It was originally proposed that gynomorphs elicit greater sexual response from males than do andromorphs, and that after their first matings, gynomorphs are more strongly subjected to fitness-reducing interactions with mate-seeking males. Under this scenario, gynomorphs and andromorphs may trade-off the costs of sexual

harassment with conspicuousness to predators and/or the risk of remaining unmated. It is still controversial whether such sexual harassment occurs, how much impact it has on female fitness, and whether avoidance of sexual harassment alone could maintain *Ischnura* female polymorphism (Sherratt 2001; Sirot & Brockmann 2001; Sirot et al. 2003; Fincke 2004; Rivera & Sánchez-Guillén 2007). Based on recent work, however, it is generally accepted that intensity of sexual harassment is frequency dependent rather than form dependent. Therefore, more common female forms should face greater sexual harassment irrespective of their specific form.

Following the *Ischnura* example, sexual harassment avoidance has most notably been invoked to explain female polymorphism in *Papilio dardanus* (Cook et al. 1994). The *P. dardanus* population on Pemba Island, Tanzania, has a single nonmimetic male form and three female forms: form *hippocoonides* mimics *Amauris niavius*, form *trimeni* is nonmimetic and male-like, and form *lamborni* is nonmimetic and dissimilar to males (Cook et al. 1994). Their relative proportions in the population differ greatly, with *hippocoonides* being the commonest (80% of the female population) and *lamborni* being the rarest form (4% of the female population). Cook et al. conducted male mate preference experiments in which they offered pinned (dead) specimens of different female forms to free-ranging males, and recorded which female form was approached first, and how long the males courted or tried to mate with the pinned females.

Cook et al. realized that in the context of female polymorphism in Pemba Island *P. dardanus*, the sexual harassment avoidance hypothesis predicted that males should approach the most common *hippocoonides* females more frequently. On the contrary, the pseudo-sexual selection hypothesis predicted that males should approach male-like *trimeni* females more frequently. Males were, in fact, found to have a preference hierarchy: *hippocoonides* females were preferentially approached and courted, followed by *trimeni* females and then *lamborni* females, exactly matching the relative frequencies of the three female forms in the population. The most parsimonious explanation for these results is that male mate preference is frequency dependent. However, from this the authors speculated that male preference of *hippocoonides* females would translate into sexual harassment, and that female polymorphism in *P. dardanus* could be maintained by frequency-dependent sexual harassment faced by different female forms. In the absence of a direct test and a logical connection between male approach rates and female fitness reduction under natural population densities, the hypothesis remains open to debate even in the case of *P. dardanus*. Moreover, this hypothesis cannot explain why different female forms have such skewed relative frequencies in the population.

The *P. dardanus* and *P. glaucus* studies highlight the problem of interpreting results of experiments that use surrogate measures instead of directly testing key predictions of the sexual selection hypotheses. Whereas 'male mate preference' proponents concluded that the female form carrying more spermatophores was favoured by sexual selection, 'sexual harassment avoidance' proponents would view this female form as being sexually harassed by males and therefore selectively disadvantaged. Instead, the relative fitness of the various female forms should be measured directly. It is also essential to show that sexual harassment indeed occurs and it has the presumed fitness-reducing impact on the commoner female form.

Understanding male mate preference at mechanistic and selectionist levels will also be important. In most behavioural studies of insects, mate preference is assumed to be innate and outside the realm of learning or other external influences such as frequency dependence. A male with an innate mate preference, and absence of learning, would thus miss a mating opportunity if it

encounters a virgin female that does not match its innate template of a 'preferred mate' (Owens & Rowe 1999; Widemo & Sæther 1999). Innate male mate preference will be particularly disadvantageous in polymorphic mimetic species such as *P. dardanus*, *P. polytes*, *P. memnon* and *H. misippus*, in which relative frequencies of different female forms may fluctuate temporally or spatially, and in which the presence and relative frequencies of female forms varies in different populations over their distributional ranges (Wallace 1865; Eltringham 1910; Wynter-Blyth 1957; Sheppard 1962; Edmunds 1966; Clarke et al. 1968, 1985; Clarke & Sheppard 1971, 1972; Smith 1984). It would also be disadvantageous when a novel mimetic female form is sweeping through the population. In such polymorphic mimetic species, male mate preference based on learning from frequency-dependent encounters with females (Van Gossum et al. 1999, 2001), or to a lesser degree imprinting (Owens & Rowe 1999), may be favoured. Currently, the extent to which male mate preference in polymorphic butterflies is innate, learned or plastic is unknown. If male mate preference is plastic, it may be influenced by relative frequencies of different female forms. The *P. dardanus* study of Cook et al. (1994) has indeed shown that male mate preference is not for the male-like form when that form is rare. It instead demonstrates preference for the most common female form (in this case the mimetic *hippocoonides* form), which must be frequency dependent since the proportion of female forms in different *dardanus* populations varies, with form *hippocoonides* being absent in some populations. It is possible that, if sexual selection initially favours nonmimetic females when male encounters with the new mimetic female form are rare, sexual selection decelerates the establishment of the mimetic female forms. After the mimetic female forms have passed the initial resistance of male mate preference, however, male mate preference should have little influence on the near-equilibrium dynamics of female polymorphism (Makielski 1972; Levin 1973).

Biologists also need to reach a consensus on whether visual male mate preference really acts as a strong sexual selective force on female wing colour patterns in butterflies. Many biologists assume that male mate preference is weak when explaining the evolution of female-limited mimicry (Brower 1963; Belt 1874; Turner 1978) but very strong when explaining the evolution of female-limited mimetic polymorphism (Burns 1966; Cook et al. 1994), even though female-limited mimicry and polymorphism co-occur in a majority of species (Kunte 2008). Resolving this contradiction is a critical step in solving the problem of female-limited mimetic polymorphism. Among the few studies conducted on Batesian mimics as well as Müllerian co-models (Müllerian co-models resemble each other but they are all unpalatable), some showed strong visual male mate preference whereas others showed it to be weak (Brower 1963; Krebs & West 1988; Cook et al. 1994; Lederhouse & Scriber 1996; Jiggins et al. 2001; Kronforst et al. 2006; Estrada & Jiggins 2008). It is important to note while interpreting these results that sexual encounters are usually much more frequent in the confined and crowded greenhouse conditions where most experiments are carried out; where males can afford to be choosy. Nevertheless, in all these experiments, each tested female and female form was courted and mated when mating was allowed, indicating that males relax their preference, if any, under repeated encounters with less preferred females. It is entirely possible that in nature, where males are greatly limited by the number of virgin or otherwise receptive females they encounter (Burns 1968), males have little opportunity to exercise any coloration-based mate preference.

In summary, in recent decades biologists have focused on sexual selection hypotheses to explain mimetic female polymorphism. However, the most important predictions of these hypotheses have been tested only indirectly and the empirical results have been

suggestive at best, but sometimes negative or inconclusive. Further experiments that directly test the predictions may remedy some of these problems. However, the limitations of male mate preference (especially if natural selection overwhelmingly favours mimetic forms and male mate preference changes under dynamic relative frequencies of female forms) and conflicting views of specific mechanisms (male mate preference versus sexual harassment) that govern the impact of sexual selection as the balancing force would still persist. These compel us to consider non-sexual selective hypotheses, particularly those based on ecological parameters.

ECOLOGICAL–PHYSIOLOGICAL TRADE-OFFS

According to this hypothesis, mimetic females trade off an unspecified physiological cost of mimicry with decreased predation risk (Ohsaki 2005). The former entails a shorter life span for mimetic females, while the latter allows them to forage and reproduce more actively than nonmimetic females. This intuitively appealing and deceptively simple ‘trade-offs’ hypothesis is fraught with ambiguities. First, it is uncertain about physiological costs of mimicry. Ohsaki (2005) lists the production of physiologically expensive wing scale pigments as the only likely cost of mimicry. While such a cost is possible in some cases, this does not appear to be a general physiological constraint on all mimetic female forms for the following reasons. Mimetic resemblance is sometimes achieved by slight modifications of wing colour and pattern elements already present in nonmimetic forms (Nijhout 1991, 2003), so these modifications may be costly in some cases but not in others. Changes in wing pigmentation also need not involve extra energy expenditure if alternative pigments are physiologically equally costly or if there are balancing advantages. For example, melanic wing scales may be costly (Stoehr 2006) and investment in them may affect immunocompetence (Lindsey & Altizer 2008). However, investment in melanic scales simultaneously has a major functional and selective advantage in thermoregulation since melanic scales help raise butterfly body temperature quickly in cooler environments (Watt 1968, 1969; Shapiro 1976; Kingsolver 1987, 1995a, b; Kingsolver & Wiernasz 1991). Thus, the sum of various advantages and disadvantages of specific pigmentation changes is critical. Given the myriad types of colour changes between nonmimetic and mimetic forms, it is statistically unlikely that changes towards mimetic coloration always involve investment in physiologically more costly pigments (e.g. a few mimetic female forms in Fig. 1 show increased wing melanization but other forms show reduced wing melanization). It is also possible that mimetic females have other physiological advantages. For example, mimetic butterflies fly slowly and need not spend greater energy on the usually hurried flight of nonmimetic butterflies, so the mimics may save a substantial amount of energy during flight (Chai & Srygley 1990). It is then uncertain whether and to what extent mimicry reduces adult physiological life span.

The trade-offs hypothesis is equally uncertain about the benefits of increased longevity accruing to nonmimetic females. It is well known that, although the sex ratio of most butterflies at eclosion is ~1:1, males are encountered in nature much more frequently than females (in Darwin 1874, pp. 259–261). This perceived skewed sex ratio is often attributed to the secretive nature of females (Owen 1974). It is speculated that females avoid detection because, if attacked, they are less likely to escape aerial-hunting insectivorous birds because of their heavier egg-laden bodies and poor escape flight (Wallace 1865; Chai & Srygley 1990; Ohsaki 1995). Thus, the risk of predation presumably severely restricts the amount of time nonmimetic females spend on activities such as feeding and oviposition. Ohsaki (2005) implied that since mimetic females are released from the intense risk of predation, they spend a greater proportion of time actively foraging and reproducing compared to

the nonmimetic females. It follows that the mimics can potentially lay an equal number of eggs in a shorter but more active life span compared to the long-living, less active nonmimics. Ohsaki, unfortunately, did not study patterns of oviposition and fecundity in the two female forms, so the trade-off implicit in this hypothesis has not actually been demonstrated. Taken together, these factors suggest that mimetic female forms may actually have a relative physiological or reproductive advantage over nonmimetic females, rather than a disadvantage. Clearly, some other ecological factor(s) must weigh against mimetic female forms and prevent them from replacing nonmimetic or other mimetic female forms in the population, thus maintaining female polymorphism.

FREQUENCY-DEPENDENT ADVANTAGE OF MIMICRY

This is the oldest and arguably the most obvious hypothesis for the maintenance of female-limited polymorphism in Batesian mimicry. It relies on the basic tenet of mimicry theory, that the advantage of mimicry is frequency dependent. At low frequency, Batesian mimics face low predation pressure and have higher fitness compared to nonmimics, and this fitness difference declines as mimic frequency increases because predators encounter more mimics at higher frequency and learn to accept them as palatable prey (Brower 1960; Huheey 1964, 1988; Ruxton et al. 2004). While building a case for mimicry theory, Bates had first observed that Neotropical butterfly mimics are usually less numerous than their models, taking it as a proof of frequency-dependent advantage of mimicry (Bates 1862). Although it is not necessary that models outnumber mimics for Batesian mimicry to be effective, a large body of observational and experimental data now shows that model–mimic frequency dynamics and predator learning limit the frequency-dependent selective advantage of mimicry and influence the presence and distribution of mimics in varied mimicry systems (Brower & Brower 1962; Smith 1973; Brodie & Brodie 1980; Brodie 1981; Nonacs 1985; Lindström et al. 1997, 2004; Pfennig et al. 2001; Harper & Pfennig 2007; Rowland et al. 2007; Ries & Mullen 2008). Thus, Batesian mimicry loses its fitness advantage at higher mimic frequencies, at which nonmimetic competitors may have greater fitness.

This type of frequency-dependent mimetic advantage may influence fitness in a sex-specific manner such that female-limited mimicry may be favoured either from the greater mimetic advantage to females or from sexual constraint on male wing coloration (Ohsaki 1995; Turner 1978; also see Introduction). Following the evolution of female-limited mimicry, the fundamental rules of frequency dependence will govern the evolution and maintenance of female polymorphism in Batesian mimicry systems as follows. (1) If the entire female prey population is small relative to the model population or if the model is highly toxic, the mimetic females will always have a fitness advantage over the nonmimetic females. This is because the mimics will never reach a frequency high enough to face the negative consequence of frequency dependence. Under this scenario, the mimetic females will completely replace the nonmimetic females in the population, and there will be no female polymorphism (Sheppard 1962). (2) If, however, the female prey population is large and exceeds the frequency-dependent limit at which mimetic females can replace the nonmimetic females, the frequencies of mimetic and nonmimetic females in the population will be held at a critical equilibrium at which their fitness is equal. This will give rise to a mimic–nonmimic female polymorphism (Barrett 1976). (3) Beyond this equilibrium point, the frequency of mimetic females can rise only if some mimics switch to mimicking a different model. This will produce multiple mimetic female forms in the population, maintaining a stable female mimetic polymorphism (Sheppard 1959, 1962). Each female form in such a polymorphic population will be

at its maximum, or 'focal', frequency (Clarke 1964; Barrett 1976). (4) The equilibrium relative frequencies of mimetic and nonmimetic female forms will be determined by several nonexclusive and sometimes interacting factors: the toxicity of models, mimetic perfection, the number of mimics mimicking a model, risk of predation from visual predators, availability of alternative nonmimetic prey, and predator attack behaviour, learning and memory (Brower 1960; Sheppard 1962; Holling 1963; Rothschild 1964; Emlen 1968; Alcock 1970; Pilecki & O'Donald 1971; Goodale & Sneddon 1977; Jeffords et al. 1979; Luedeman et al. 1981; Nonacs 1985; Hetz & Slobodchikoff 1988; Speed 1993; Pinheiro 1996; Lindström et al. 1997, 2004; Speed & Turner 1999; Holen & Johnstone 2004, 2006; Langham 2004). Generally, under the frequency-dependence hypothesis, greater relative frequency of mimics, mildly toxic models and slow-learning or forgetful predators will favour female polymorphism. Similar frequency-dependent conditions also govern polymorphism in other types of Batesian and Müllerian mimicry (reviewed in: Turner 1977; Joron & Mallet 1998; Mallet & Joron 1999; Ruxton et al. 2004).

The above discussion shows that the frequency-dependent advantage to mimicry is capable of predicting the precise ecological regimes under which mimetic female polymorphism may or may not evolve. Moreover, it can predict the equilibrium relative frequencies at which different female forms will be maintained in relation to the community context of Batesian mimicry that includes co-mimics, models and predators. It also accounts for the remarkable variation in female polymorphism mentioned in the Introduction and illustrated in Fig. 1. The first four hypotheses mentioned in this review do not possess such strong predictive power, nor do they explain mimicry in its ecological and social settings. Another advantage of the frequency-dependence hypothesis is its parsimony: it is independent of sexual selection, so it neither makes any assumptions about male mate preference nor requires balancing sexual selection to account for female-limited polymorphism (Sheppard 1962; Barrett 1976). Other hypotheses, however, depend on the basic functioning of frequency dependence in addition to their own unique assumptions.

The hypothesis, that frequency-dependent advantage of mimicry may give rise to female polymorphism by preventing a mimetic female form from replacing the nonmimetic or other mimetic female forms, was frequently mentioned during the early period of discovery and genetic work on female-limited mimetic polymorphism (Poulton 1908; Fisher 1958; Sheppard 1959, 1962). Surprisingly, then, there have been no attempts to systematically test it to date. With data on female polymorphism and model-mimic frequencies in a number of mimicry rings (a mimicry ring is an assemblage of co-occurring Müllerian co-models and Batesian mimics that share a common warning wing colour pattern), it should be, in principle, straightforward to test at least the following critical prediction of this hypothesis: female polymorphism is common in mimicry rings in which the frequency of mimics is high. The converse prediction is that female-limited mimics are not polymorphic in mimicry rings in which mimic frequencies are low (i.e. when mimics are relatively uncommon, the entire female population is mimetic).

Unfortunately, perhaps from lack of focus, comprehensive data on the relative frequencies of models and mimics in entire mimicry rings are rare. Nevertheless, from the few quantitative studies currently available, I make the following preliminary observations that support the above two predictions. In North America, in the *Battus philenor* mimicry ring, in which mimics far outnumbered the model, six of the eight Batesian mimics were female-limited, two of which were female dimorphic (Brower & Brower 1962; Pavulaan & Wright 2004). Similarly, in the West African mimicry rings surrounding toxic *Bematistes epaea* and *Acraea jodutta* females,

mimic frequency was relatively high and many mimics were polymorphic and female limited, including the classic examples *Papilio dardanus* and *Pseudacraea eurytus* (Owen 1974). On the other hand, Ecuadorean mimicry rings are dominated in terms of population size and constituent species by the highly toxic ithomiine butterflies: in one study, ithomiines made up more than 90% of the ring in six of eight mimicry rings and, interestingly, very few mimics in these mimicry rings were female limited, and almost none were polymorphic (Beccaloni 1997). Other studies have recently presented community ecological data only for the Müllerian components of mimicry rings (DeVries et al. 1999; Joron et al. 1999; Joron 2005; Elias et al. 2008), so they are not suitable to test this hypothesis. Overall, although these preliminary observations seem to support the frequency-dependence hypothesis, it would greatly benefit from a rigorous test, similar to the other hypotheses.

The above review shows that hypotheses to explain Batesian mimetic female polymorphism abound, but carefully planned studies that test key predictions of any particular hypothesis have been scarce. Most hypotheses have rarely been studied in a systematic manner, and none of the studies unequivocally support a single hypothesis. However, given its key role, frequency-dependent mimetic advantage must be considered the prime driver in the evolution and maintenance of female mimetic polymorphism. It will, therefore, be most useful to test this hypothesis before considering other hypotheses, or to treat it as a null hypothesis while testing other hypotheses. Among the five hypotheses listed above, I believe that the frequency-dependent advantage of mimicry alone will eventually account for the majority of female-limited mimetic polymorphism. Extensive field data on model-mimic frequencies and other community ecological aspects of entire mimicry rings will be crucial in testing the frequency-dependence hypothesis in the future. Although this is a daunting task, it holds the best promise of solving this problem, and recent studies on the unusually diverse ithomiine and *Heliconius* butterfly mimicry rings have shown that this is achievable (Beccaloni 1997; Joron et al. 1999; Joron 2005; Elias et al. 2008). The remaining variation that is not explained by frequency-dependent selection may be studied with multifactorial experimental designs that simultaneously test predictions of several sexual selection hypotheses. The focus should be on studying the mechanistic basis of male mate preference and to specifically test whether male mate preference is plastic, restrictive or frequency dependent. Most importantly, the relative strengths of natural and sexual selection on various female forms should be carefully studied with as direct measures of female fitness as possible. Such a stepwise observational and experimental approach may ultimately help to explain female-limited mimetic polymorphism, an iconic adaptation that has inspired extensive theoretical, genetic and experimental work in the past and continues to serve as a model of natural and sexual selection in action.

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