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Mimetic butterflies support Wallace's model of sexual dimorphism

Krushnamegh Kunte*

Section of Integrative Biology, University of Texas at Austin, 1 University Station C 0930, Austin, TX 78712-0253, USA

Theoretical and empirical observations generally support Darwin's view that sexual dimorphism evolves due to sexual selection on, and deviation in, exaggerated male traits. Wallace presented a radical alternative, which is largely untested, that sexual dimorphism results from naturally selected deviation in protective female coloration. This leads to the prediction that deviation in female rather than male phenotype causes sexual dimorphism. Here I test Wallace's model of sexual dimorphism by tracing the evolutionary history of Batesian mimicry—an example of naturally selected protective coloration—on a molecular phylogeny of *Papilio* butterflies. I show that sexual dimorphism in *Papilio* is significantly correlated with both female-limited Batesian mimicry, where females are mimetic and males are non-mimetic, and with the deviation of female wing colour patterns from the ancestral patterns conserved in males. Thus, Wallace's model largely explains sexual dimorphism in *Papilio*. This finding, along with indirect support from recent studies on birds and lizards, suggests that Wallace's model may be more widely useful in explaining sexual dimorphism. These results also highlight the contribution of naturally selected female traits in driving phenotypic divergence between species, instead of merely facilitating the divergence in male sexual traits as described by Darwin's model.

Keywords: Batesian mimicry; polymorphism; female-limited mimicry; directional selection; stabilizing sexual selection; convergence

1. INTRODUCTION

Darwin noted that, 'when the sexes of butterflies differ, the male as a general rule is the more beautiful and departs more from the usual type of colouring of the group to which the species belongs. Hence in most groups the females of the several species resemble each other much more closely than do the males' (Darwin 1874, p. 320). According to this classical view of the evolution of sexual dimorphism, male phenotypes (often sexual ornaments and weapons) diverge from ancestral forms in response to directional sexual selection, while females retain their ancestral forms under stabilizing natural selection (figure 1*a*). Darwin's model of sexual selection has been widely supported (Fisher 1958; Campbell 1972; Bradbury & Andersson 1987; Andersson 1994). Many biologists therefore believe sexual selection to be an almost exclusive selective cause of sexual dimorphism, often taking sexual dimorphism as an indirect measure of sexual selection (Barraclough *et al.* 1995) or treating them as hallmarks of each other (Read & Harvey 1989; Fitzpatrick 1994).

Nonetheless, Darwin was aware that not every sexual dimorphism was due to sexual selection. Biologists following him also acknowledge that sexes may differ due to intrinsic differences in the sexual roles of the sexes and intersexual niche diversification (Selander 1966, 1972; Hedrick & Temeles 1989; Shine 1989). Several recent studies on the evolution of sexual dimorphism in birds and lizards, however, have uncovered patterns of sexual dimorphism which do not follow the classical Darwinian model of sexual selection or other widely known phenomena: (i) selective pressures on and evolutionary changes in female, rather than male, traits frequently cause sexual dimorphism (Badyaev 2002; Badyaev & Hill 2003; Ord & Stuart-Fox 2006), (ii) in clades with sexually monomorphic, brightly coloured ancestors, sexual dimorphism may be a derived trait arising from natural selection for female protective coloration instead of sexual selection for exaggerated male traits (Burns 1998; Penz & DeVries 2002) and finally, (iii) mutual sexual selection and social competition may cause the selected traits to be sexually monomorphic, further breaking up the assumed tight association between sexual selection on male traits and sexual dimorphism (Huxley 1938; West-Eberhard 1983; Jones & Hunter 1993; Amundsen *et al.* 1997; Emlen *et al.* 2005; Clutton-Brock 2007). These findings suggest that alternative models that could explain the evolution of sexual dimorphism under different selective regimes should now be considered.

Wallace presented a contrasting view of sexual dimorphism compared with that of Darwin, emphasizing the role of natural selection on female traits. He believed that naturally selected deviation for cryptic or otherwise protective coloration in females was responsible for sexual dimorphism (Wallace 1889; figure 1*b*). Thus, the two crucial differences between the Darwin and Wallace models are (i) the type of selection that drives the phenotypic divergence, and (ii) the sex that diverges from the ancestral phenotype. Recently observed patterns of colour dimorphism in birds and lizards, mentioned

*krushnamegh@mail.utexas.edu

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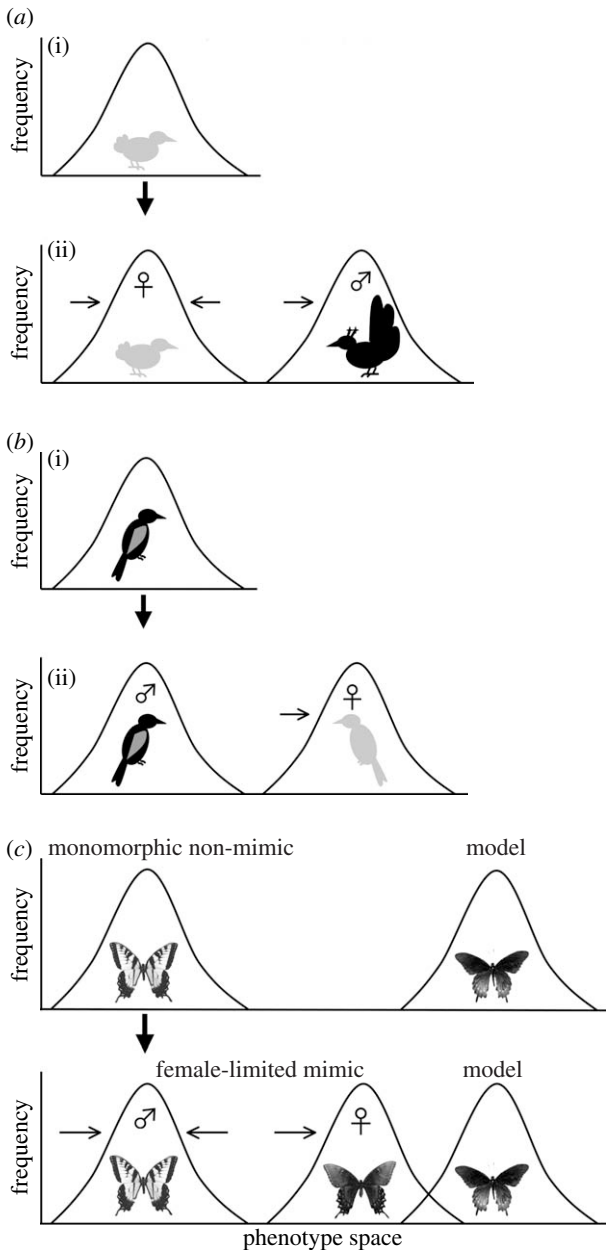

Figure 1. (*a*) Darwin's and (*b*) Wallace's model of sexual dimorphism in (i) ancestral sexually monomorphic population and (ii) sexually derived dimorphic population. (*c*) Model of the evolution of female-limited mimicry. Thin arrows indicate the direction of selection on the phenotypes and thick arrows indicate direction of evolutionary change.

above, are remarkably suggestive of Wallace's model being at work, but the model has not been tested explicitly. Here I test this model in a group of butterflies with extensive Batesian mimicry, a group that fuelled a prolonged disagreement between Wallace and Darwin on the roles of natural and sexual selection in the evolution of sexual dimorphism (Kottler 1980).

In Batesian mimicry, predation pressure on palatable prey species selects for their resemblance to species that are toxic to predators (Ruxton *et al.* 2004). Wallace noted that in many Indo-Malayan *Papilio* butterflies, mimicry was limited to females (Wallace 1865). He proposed that female-limited mimicry evolved because females, due to their very heavy egg-loads and less effective escape flights, faced greater predation risk and gained a proportionately greater advantage by mimetic resemblance compared with males (also see Ohsaki 1995). As per the Wallace model applied to female-limited mimicry, sexual dimorphism evolves under natural selection on protective (mimetic) female wing coloration: females deviate from their ancestral forms under directional natural selection to converge on the colour patterns of toxic species (known as 'models'), while males retain their ancestral patterns (figure 1*c*. Note that mimicry is an adaptive response to visual predators, hence in this paper I refer to sexual dimorphism as manifested in wing colour patterns alone, that is, by sexual dichromatism). Lesser mimetic advantage to males itself may prevent male mimicry (Wallace 1889) but additional stabilizing (mainly sexual) selection may further constrain male wing patterns in female-limited mimetic butterflies (Joron & Mallet 1998). This restrictive selection on male patterns is traditionally considered to be female choice (Belt 1874; Brower 1963; Turner 1978). However, it has been pointed out that there is scant evidence in butterflies for female mate choice for male coloration outside the ultraviolet, and most of the close-range mate choices exercised by females are based on olfactory rather than visual signals (Boppré 1984; Silberglied 1984; Vane-Wright & Boppré 1993; but also see Krebs & West 1988). Silberglied (1984) and Vane-Wright (1984) have advocated the view that males are highly visually oriented and their displays and signals largely determine outcomes of male–male interactions; therefore intrasexual interactions largely constrain male visual signals including wing colour patterns. This view has some experimental support (Lederhouse & Scriber 1996).

Although the exact stabilizing selective force on male wing colour patterns is still unclear, the phenomenon of female-limited mimicry has now been widely documented. Many evolutionary and genetic aspects of female-limited mimicry have also been theoretically elucidated and applied to problems of natural selection and Batesian mimicry (Fisher 1958; Sheppard 1960; Williamson & Nelson 1972). Nonetheless, Wallace's idea that natural selection for protective (including mimetic) female coloration may drive the evolution of sexual dimorphism has rarely penetrated discussion about the models of sexual dimorphism. It has also never been directly tested. Here I bridge this gap by analysing phylogenetic patterns of sexual dimorphism and female-limited mimicry in *Papilio* and test the predictions of Wallace and Darwin's models to study their relative contributions to sexual dimorphism in *Papilio*.

Among the 200 species of *Papilio* worldwide, sexual dimorphism and Batesian mimicry have evolved multiple times (Zakharov *et al.* 2004). In some species both sexes are mimetic; in others mimicry is female limited. Many female-limited mimics also exhibit mimic/non-mimic female polymorphism in which at least one female form is non-mimetic (very often male-like), and at least one female form is mimetic (Wallace 1865; Wickler 1968; Mallet & Joron 1999). Although female polymorphism also occurs outside of mimicry (Magnus 1963; Graham *et al.* 1980), a combination of frequency-dependent advantages of Batesian mimicry (Turner 1978; Ohsaki 1995), physiological trade-offs of being mimetic or non-mimetic (Ohsaki 2005) and the mating advantage of being non-mimetic (Burns 1966; Vane-Wright 1984; Lederhouse 1995; but also see Platt *et al.* 1984 and references therein) raises the possibility that female-limited mimicry fosters the

evolution of female polymorphism more than any other factors under which female polymorphism might evolve. Finally, some *Papilio* species are remarkably brilliantly coloured, undoubtedly due to sexual selective pressures. Overall, the colour patterns, mimicry and polymorphism in *Papilio* are very diverse, which have evolved under complex selective pressures (Vane-Wright 1975, 1976*a*, 1979), which I will fully describe in a phylogenetic context in a separate paper.

The diversity of mimicry-related characters and bright wing coloration in *Papilio* enables a test of Darwin and Wallace's models of sexual dimorphism and their relative importance in *Papilio*. A tendency in female wing coloration to deviate towards novel mimetic patterns would support Wallace's model, whereas a tendency in male wing patterns to deviate towards novel brilliant coloration would support Darwin's model. Thus, Wallace's model predicts an association between sexual dimorphism and female-limited Batesian mimicry, whereas Darwin's model predicts an association between sexual dimorphism and bright wing patterns only in males. Phylogenetic associations between sexual dimorphism, female-limited mimicry and female polymorphism would further support Wallace's model since in both female-limited mimicry and female polymorphism females deviate from ancestral patterns. I tested these predictions by mapping sexual dimorphism, deviation in female versus male wing patterns, presence of mimicry, sex limitation of mimicry and female polymorphism on a published molecular phylogeny of *Papilio*. My analysis bolsters the view that natural selection on female phenotype may be a frequent cause of sexual dimorphism.

2. MATERIAL AND METHODS

(a) *Molecular phylogeny of* Papilio

I used a published *Papilio* phylogeny generated with data from approximately 2.3 kilobases (kb) of mitochondrial genes (cytochrome oxidase subunits I and II and tRNA leucine) and approximately 1.0 kb of nuclear protein-coding genes (EF-1α), using maximum parsimony, maximum likelihood and Bayesian analyses implemented in PAUP* and MrBayes (Zakharov *et al.* 2004). It included 51 *Papilio* species (approx. 25% of the global total) representing all major species groups and two outgroups: *Pachliopta neptunus* and *Eurytides marcellus*.

(b) *Wing colour patterns, sexual dimorphism and ancestral phenotypes*

Most species groups in *Papilio* (summarized in Zakharov *et al.* 2004) usually have wing colour patterns with characteristic background coloration and an arrangement of spots and bands, which may be strikingly divergent between sister groups (personal observations; electronic supplementary material, figure 1). This enabled me to study which sex in dimorphic species had deviated from the colour patterns of its species group, that is, from its ancestral wing colour pattern.

(c) *Character assignment*

Character states were assigned from specimens deposited in the McGuire Center for Lepidoptera and Biodiversity in the University of Florida at Gainesville. All character states were unordered and unweighted. Subspecific and geographical variation was included in specific character assignments. I mapped the following characters related to sexual dimorphism, mimicry and sex limitation of mimicry. (i) Sexual dimorphism: I considered species dimorphic only when wing colour patterns of the sexes differed unsubtly. This classification was based on colour patterns in the spectral range visible to humans. I did not consider sexual dimorphism in ultraviolet reflectance (Silberglied 1979), which apparently does not differ between mimetic and non-mimetic morphs (Remington 1973; Silberglied 1979). (ii) Deviation of female colour pattern from the ancestral pattern: this was determined by studying whether or not the wing colour pattern of at least one female morph in sexually dimorphic species deviated from ancestral pattern. It follows that if female wing colour pattern did not deviate from the ancestral pattern, then deviation in male pattern caused sexual dimorphism. (iii) Female polymorphism. (iv) Presence of Batesian mimicry. (v) Female limitation of mimicry.

(d) *Phylogenetic analyses of character evolution and associations*

I studied the character evolution by reconstructing ancestral states using maximum likelihood criterion with one-parameter Markov *k*-state model implemented in Mesquite (Maddison & Maddison 2006). I tested the correlations between the characters with Pagel's correlation test (Pagel 1994) in Mesquite, which uses two binary characters and compares the ratio of likelihoods of two models: one in which the rates of change in each character are independent of the state of the other, and the other in which the rates of change depend on the state of the other character. The significance of the ratio was tested with 1000 simulations.

3. RESULTS

Papilio is predominantly a sexually monomorphic and non-mimetic group, in which sexual dimorphism, female-limited mimicry and female polymorphism have evolved multiple times (figure 2). Sexual dimorphism is correlated with both female-limited mimicry (log-likelihood: 4 parameter model, −60.26; 8 parameter model, −40.7; difference, 19.56; $p<0.001$; figure 2*a*,*b*) and with the deviation of female wing colour patterns from the ancestral patterns (log-likelihood: 4 parameter model, −63.77; 8 parameter model, −35.41; difference, 28.36; $p<0.001$; figures 2*a*,*c* and 3). Both associations support Wallace's model of sexual dimorphism, as they show that deviation in female patterns towards mimetic coloration has contributed to most sexual dimorphism in *Papilio*.

Female polymorphism is correlated with female-limited mimicry (log-likelihood: 4 parameter model, −55.8; 8 parameter model, −40.2; difference, 15.6; $p<0.001$; figure 2*b*,*d*). This correlation indicates that female polymorphism is more probable when female-limited mimicry is present in a species. Most of the female polymorphisms in *Papilio* are of mimic/non-mimic type, with numerous female forms in some species diverging from ancestral male-like wing colour patterns to mimic multiple models (e.g. *Papilio polytes* in electronic supplementary material, figure 1). Species in which sexual dimorphism, female-limited mimicry and female polymorphism were not correlated (pointed out in figure 2 with arrows) are notable for various reasons. *Papilio nobilis* and *Papilio phorcas* are unusual in many ways, as discussed below. *Papilio erostratus* sexes are dimorphic but mimetic:

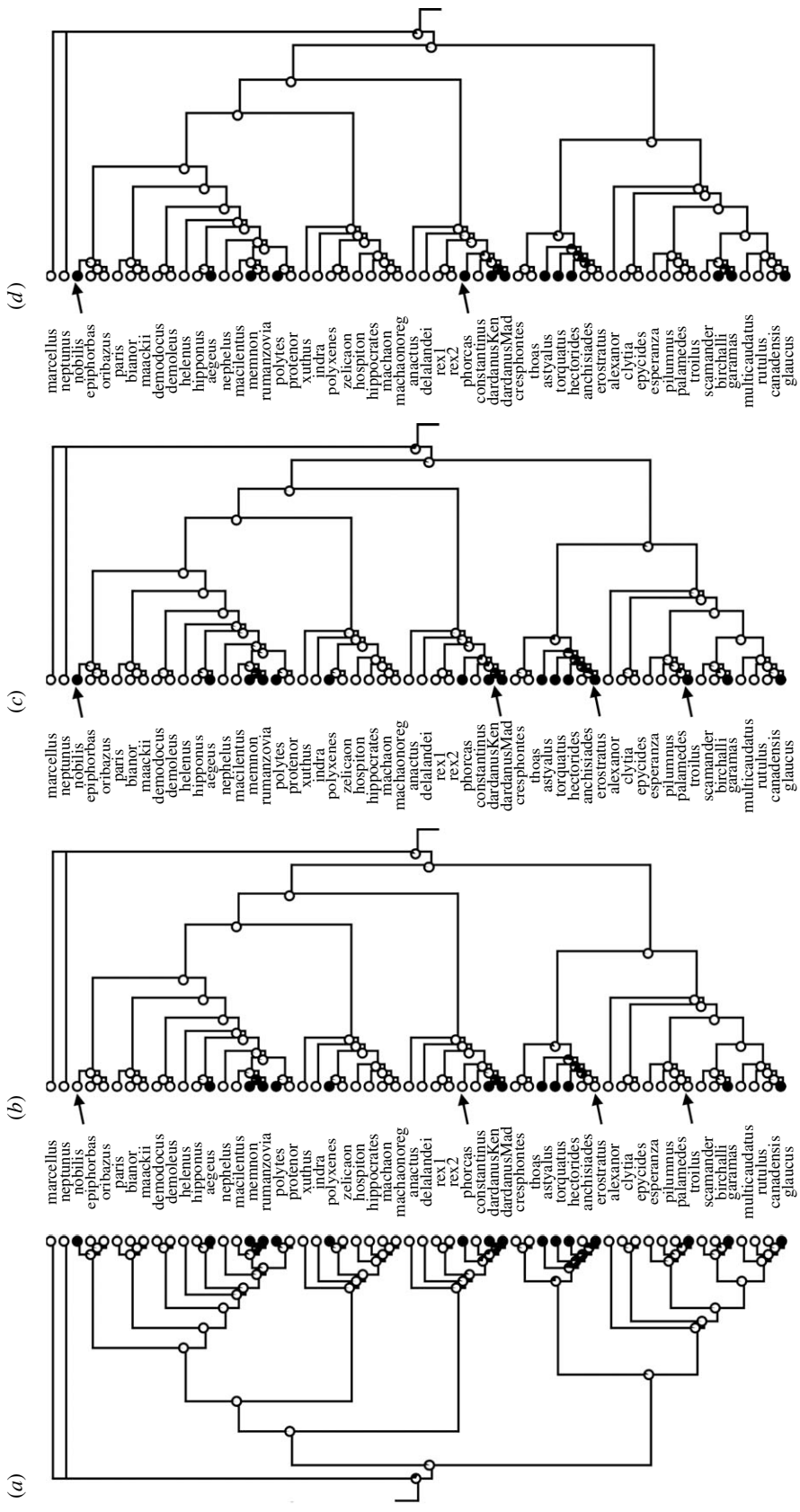

Figure 2. (*a*) Correlation of sexual dimorphism (open circles, sexually monomorphic species; closed circles, sexually dimorphic species) with (*b*) female-limited mimicry (open circles, species without female-limited mimicry; closed circles, female-limited mimics),(*c*) deviation in female wing colour patterns (open circles, female patterns not divergent; closed circles, female patterns divergent from ancestral patterns) and (*d*) female polymorphism mapped on a molecular phylogeny of *Papilio* butterflies (open circles, females not polymorphic; closed circles, females polymorphic). Internal nodes show maximum likelihoods for the character states. See the text for species pointed out with arrows.

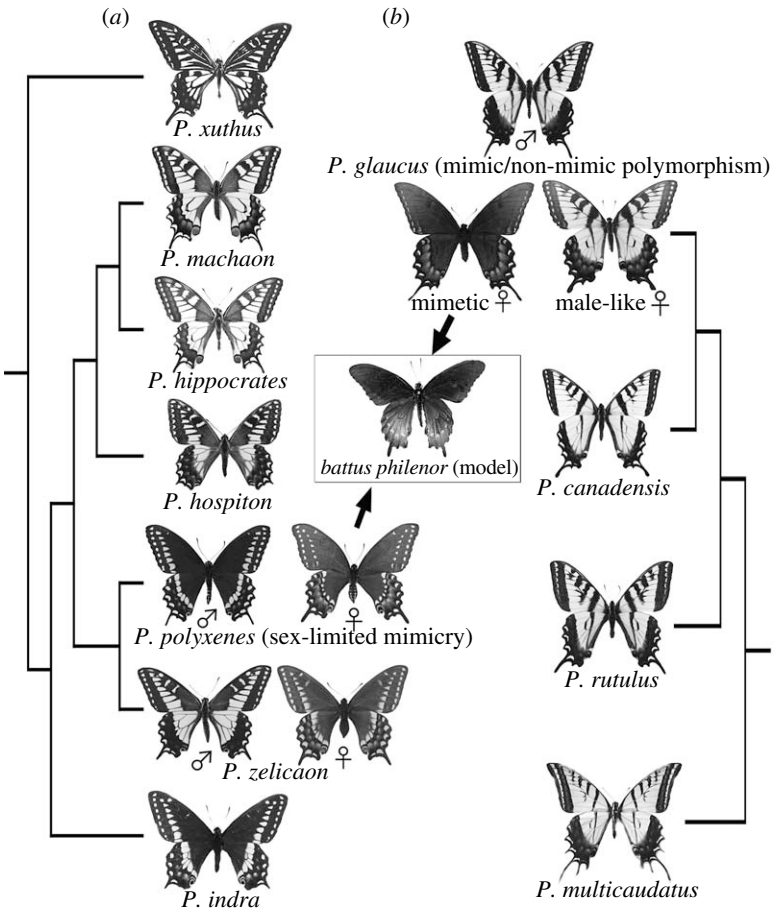

Figure 3. Exemplary patterns of female-limited mimicry and polymorphism traced on the phylogenies of (*a*) *Papilio machaon* and (*b*) *P. glaucus* species groups, demonstrating naturally selected deviations in female coloration. Mimetic females have melanic patterns with reduced yellow and increased blue on the wings, bringing about mimicry of toxic *B. philenor*. Males exhibit variations on the colour patterns of the species group. Sexes of only sexually dimorphic species are illustrated separately (also see electronic supplementary material, figure 1).

females mimic *Parides photinus* while males mimic *Battus polydamas*. *Papilio troilus* is also sexually dimorphic with both sexes mimicking *Battus philenor*. In this unusual species males have maintained weakly mimetic, divergent wing patterns, which may be considered as an example of sexually selected trait. Female *P. troilus* are more convincing mimics. Apart from these exceptions, the overall patterns of female-limited mimicry and polymorphism in *Papilio* strongly support Wallace's model of sexual dimorphism, as shown above.

4. DISCUSSION

Following Darwin's forceful advocacy of sexual selection and its subsequent support by others, most biologists tend to believe that natural selection on female traits is an insignificant source of sexual dimorphism. Silberglied reviewed the differences in Darwin and Wallace's views on sexual selection and dimorphism, particularly in relation to wing coloration in butterflies. He concluded, 'Wallace (1889) believed that the sexual dimorphism exhibited by many butterflies was often due to the acquisition of protective coloration by females, rather than to the development of brilliant colours in males by intersexual selection. However, the diversity of brilliant patterns of the males and the similarity of closely related females argue strongly against this view, suggesting that protective coloration represents an ancestral character state that existed before the evolution of brilliant dorsal wing displays.' (Silberglied 1984, p. 208). Silberglied's is the prevalent notion about butterfly wing colour patterns, consistent with Darwin's model but not in agreement with the evidence presented for *Papilio*. The *Papilio* case instead shows that the Wallacean process of sexual dimorphism can be predominant in some groups. Outside of *Papilio*, female-limited mimicry has resulted in sexual dimorphism in a large number of tropical nymphalid and pierid butterflies. However, evidence for Wallace's model is not restricted to Batesian mimicry. For example, in the neotropical non-mimetic *Morpho*, sexually monomorphic brilliantly coloured wing patterns are ancestral and widespread, while cryptic female patterns are derived and have evolved at least twice, giving rise to prominent sexual dimorphism (Penz & DeVries 2002). It would be unfortunate to ignore other groups of nymphalid butterflies in which patterns of sexual dimorphism are suggestive of Wallacean process. A detailed analysis of sexual dimorphism in a larger butterfly phylogeny would be particularly illuminating in revealing the true extent of sexual dimorphism resulting from either Wallacean or Darwinian processes.

Note that only approximately 25% of *Papilio* species were represented on the phylogeny I used, and taxon sampling profoundly affects conclusions of phylogenetic analyses (Santos *et al.* 2003). A comprehensive survey of sexual dimorphism and mimicry in Asian and

American *Papilio*, however, suggests that a denser phylogeny of *Papilio* would actually support Wallace's model more strongly because (i) sexually dimorphic *Papilio* not represented on the current phylogeny are mostly female-limited mimics, and (ii) deviation in male phenotype is rarer in *Papilio* than suggested by the present analysis (Corbet & Pendlebury 1992; Pinratana & Eliot 1992; Tyler *et al*. 1994).

As expected under Wallace's model of sexual dimorphism, most sexually dimorphic *Papilio* analysed here were female-limited mimics with males representing ancestral wing colour patterns, and females deviating towards novel mimetic coloration (figures 2 and 3). The two prominent exceptions were African *P. nobilis* and *P. phorcas*, which followed Darwin's model of sexual dimorphism. These species are sexually dimorphic with the males boldly marked but their sexual dimorphism is not related to mimicry. The *phorcas* species group with its iconic mimetic member *Papilio dardanus* is of special historical interest (Poulton 1914; Sheppard 1960; Ford 1964; Vane-Wright 1976*b*; Nijhout 2003). Sexual dimorphism in the non-mimetic *P. phorcas* and the closely related *Papilio pelodurus* and *Papilio mangoura* (not included in the phylogeny) evolved from monomorphic, non-mimetic ancestral wing patterns of the species group, represented in electronic supplementary material, figure 1 by *Papilio constantinus*. The sexual dimorphism initially evolved due to sexual selection on male wing colour patterns, which are divergent in this group, the females representing the ancestral pattern. This was followed by female dimorphism in *P. phorcas*, in which one female form was ancestral, and the newly evolved male-like form (see electronic supplementary material, figure 1) was presumably acquired due to 'pseudo-sexual selection' on females to gain mating advantage (Vane-Wright 1984). This was apparently brought about by secondary gain of male-like pattern through 'transvestism' (Vane-Wright 1976*b*; Clarke *et al*. 1985). Later, in *P. dardanus* apomorphic changes in the wing coloration of both sexes accompanied the evolution of female-limited mimicry and both-sex non-mimetic wing coloration (Vane-Wright *et al*. 1999). Bright wing colour pattern of male *P. dardanus* is divergent from its sister species, and females show a mimic/non-mimic polymorphism with a male-like non-mimetic form and several mimetic forms that mimic distantly related danaine and acraeine models (Nymphalidae; electronic supplementary material, figure 1). Thus, in *P. dardanus*, the changes in male coloration towards novel patterns are due to sexual selection, the evolution of mimetic female patterns is under natural selection, and the evolution of male-like female form, if it is derived, may have resulted from pseudo-sexual selection. The case of sexual dimorphism in the *phorcas* group, particularly the interaction of various selective forces in *P. dardanus*, is intriguing but in no sense typical of *Papilio*. This unusual group rather underlines the fact that, with a few exceptions, sexual dimorphism in *Papilio* has evolved almost exclusively due to the deviation of female wing patterns for female-limited mimicry, with males representing the ancestral patterns.

In reviewing recent studies in which patterns of sexual dimorphism have been analysed in a phylogenetic context (e.g. *Papilio* butterflies, tanagers (Burns 1998) and dragon lizards (Ord & Stuart-Fox 2006)), it seems that selection pressures vary among different species groups such that in some taxa sexual dimorphism has evolved mainly due to sexual selection on males, and in others mainly due to natural selection on females. Thus, sexual dimorphism stemming from sexual selection may be pervasive, but the plurality of models of sexual dimorphism seems to be not only appropriate but also necessary to explain the full gamut of sexual dimorphism evident in nature. Wallace's model may be more widely applicable than previously thought and deserves further studies in a wider array of taxa from diverse ecological, evolutionary and genetic backgrounds. Theoretical development based on the recent findings would be valuable in advancing our understanding of the selection regimes and genetic backgrounds on which either natural or sexual selection on males or females is more likely to contribute to the evolution of sexual dimorphism.

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