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Wing shape variation in the mimetic butterfly *Papilio dardanus* (Papilionidae) and its unpalatable nymphalid models

Miles Hegedus
University of New Orleans, mhegedus@uno.edu

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Wing shape variation in the mimetic butterfly *Papilio dardanus* (Papilionidae) and its unpalatable nymphalid models

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Master of Science
in
Biological Sciences

by

Miles Hegedus

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Abstract

Papilio dardanus displays female-limited polymorphic mimicry of multiple model species. Butterfly wing shape is species-specific and can influence mimetic signaling, but has not been characterized in this species. We used elliptical fourier analysis to investigate whether mimetic *P. dardanus* female forms have converged on the wing shape of their respective models. Although both models and mimics varied in forewing and hind wing shape, we found no evidence of forewing shape convergence between them. Overall, forewings did not differ in shape between sexes in *P. dardanus*, nor in four non-mimetic *Papilio* used for comparison. Similarly, there were no hind wing differences between the sexes in the four non-mimetic *Papilio*. However, *P. dardanus* hind wings varied significantly between mimetic females and non-mimetic individuals suggesting that, in addition to wing color pattern, the evolution of mimicry has led to changes in hind wing shape in *P. dardanus*.

Keywords: *Papilio dardanus*, Batesian mimicry, female-limited polymorphism, wing shape.

Introduction

Predation is a selective force that can shape adaptations, of which mimetic convergence is an iconic example. Batesian mimicry, the resemblance of unprotected species to defended models, has evolved independently in various plants and animals (Brodie, 1993; Johnson, 1994; Kuchta et al., 2008), including moths and butterflies (Lepidoptera). Many species of butterflies sequester or synthesize chemical compounds that decrease their palatability to predators (Brower et al., 1967). Unpalatable butterfly species usually advertise their defense with distinctive, memorable, aposematic wing color patterns (Bates, 1862; Chai, 1986), and their palatable mimics can be considered pattern parasites because they potentially decrease the effectiveness of the model's color signal (DeVries, 1987; Lehmann et al., 2014; Pinheiro et al., 2016). Female-limited Batesian mimicry is of particular interest because it implies that selection can operate differentially on male and female wing color pattern and morphology.

The African mocker swallowtail, *Papilio dardanus* Brown (Papilionidae), exhibits strong sexual dimorphism and female-limited mimicry. Throughout their range from the rainforests of West Africa through the Great Rift Valley and the islands of Madagascar and Comoros, non-mimetic males are black and yellow with slight variations between subspecies, and all possess hind wing tails (Fig. 1). The highly polymorphic females are Batesian mimics of chemically protected species in the tribes Danaini and Acraeini (Trimen, 1869; Ford, 1936), which are distantly related within the Nymphalidae (Wahlberg et al., 2009) and that vary in color pattern, wing shape, and size (Fig. 1). Mimetic females of *P. dardanus* usually lack hind wing tails and display various distinct wing color patterns, often in sympatry, and offspring from the same female can possess different color forms (Clarke & Sheppard, 1959). In Ethiopia, Madagascar, and Comoros, females have the same wing pattern as the male, including hind wing tails (Fig. 1). *Papilio dardanus* is composed of at least ten allopatric subspecies, five of which include multiple female mimetic color forms (Thompson, 2014; Table 1; see also Ford, 1936 and Clarke & Sheppard, 1959, 1960c). Based on mitochondrial DNA markers, Clark & Vogler (2009) suggested that *P. dardanus* is composed of two lineages corresponding to western and eastern mainland Africa, plus two from Madagascar and surrounding islands (nuclear markers revealed no geographic structure).

The diversity of color forms and hind wing tail polymorphism sparked an interest in the genetics of female-limited mimicry in *P. dardanus*. Whole-pattern inheritance is considered to be controlled by a suite of tightly linked genes at the *H* locus, referred to as a supergene by Clarke & Sheppard (1960b). Early experimental crosses revealed that mimetic color patterns are inherited in Mendelian ratios, indicating a single-locus control of color pattern that adheres to a predictable dominance hierarchy (Clarke & Sheppard, 1959). The role of locally adapted modifier genes was revealed after crosses between subspecies produced a breakdown of mimicry in hybrid offspring (Clarke & Sheppard, 1960a). Hind wing tail development is controlled by a separate locus, with the recessive allele for tail-development being fixed in the few populations exhibiting male-like females (Clarke & Sheppard, 1960d).

Recent research on *P. dardanus* has taken two complementary paths: establishing the functional control of genes that determine the distinct female color forms, and uncovering the evolutionary

origin of female-limited mimicry (Nijhout, 2003; Clark et al., 2008; Clark & Vogler, 2009; Timmermans et al., 2014). Comparative genomics confirmed that mimicry is controlled by the *H* locus, and suggested that transcription factor genes *engrailed* and *invected* have a regulatory role (Timmermans et al., 2014; Clark et al., 2008). From a phylogenetic standpoint, consideration of close relatives might shed some light on the evolution of mimicry in *P. dardanus*. DNA-based analyses placed the sexually dimorphic *P. phorcas* as sister to *P. dardanus* (Vane-Wright et al., 1999; Clark & Vogler, 2009). Based on these relationships, Clark & Vogler (2009) hypothesized that, as an ancestral condition, sexual dimorphism led to the evolution of female-limited mimicry in *P. dardanus*. These authors also hypothesized that female-limited mimicry is an ancestral condition within *P. dardanus* because male-like females did not cluster together nor constituted early lineages in the tree. Note, however, that a previous analysis including 51 *Papilio* species placed *P. constantinus*, not *P. phorcas*, as the sister species of *P. dardanus*, and suggested that female-limited mimicry evolved independently at least seven times within *Papilio* (Zakharov et al., 2004).

Color pattern resemblance is one of several attributes that contribute to mimicry. Field experiments by Chai (1986, 1990) indicated that insectivorous birds use not only wing color but also flight pattern to discriminate among butterfly species. His bio-assays examined the responses of the rufous-tailed jacamar (Galbulidae) to butterflies that varied in palatability, color pattern, sexual dimorphism, and mimicry. His work stimulated comparative research on how wing and body morphology relate to flight (Chai & Srygley, 1990; Srygley & Chai, 1990; Marden & Chai, 1991; Srygley, 1999; Srygley & Ellington, 1999a, b). Non-mimetic, palatable butterflies typically rely on fast or erratic flight for escaping predators, which requires higher mass allocation to flight muscle and also wing shape adaptations (Chai, 1986, 1990; Marden & Chai, 1991). In contrast, the flight pattern of unpalatable butterflies tends to be slower and more predictable (but see Pinheiro et al., 2016), which aids in the visual effect of their defensive wing colors. Mimics could therefore be expected to converge not only on the wing colors of their models, but also on their flight pattern (Chai, 1986; Srygley 1994, 1999). The investigation of a possible association between wing color and shape is therefore relevant to studies of mimicry because, among other factors, wing aerodynamic properties can influence flight performance (see Dudley 2002 for a review). Indeed, Jones et al. (2013) investigated a possible wing shape association between color morphs of the locally polymorphic *Heliconius numata* (Nymphalidae, Heliconiini) and its mullerian comimics in the genus *Melinaea* (Nymphalidae, Ithomiini). Their analyses showed wing shape sexual dimorphism in *H. numata*, and among the three examined color forms and their comimics they showed a wing shape correspondence between *H. numata* f. *silvana* and *M. ludovica ludovica* only. This finding led Jones et al. (2013) to raise the possibility that the supergene determining wing color pattern might also influence wing shape.

In addition to divergent color patterns, female-limited mimicry opens a possibility for the evolution of wing shape sexual dimorphism. *Papilio dardanus* is a suitable focal organism to investigate the association between wing color and shape because females not only converge onto models that vary in both these attributes, but in some localities they are non-mimetic (male-like). Accordingly, we use morphometric analysis to compare wing shapes of *P. dardanus* female color forms and their respective model species, and discuss the role of mimicry on wing

shape. We examined forewings and hind wings separately to address the following questions: (1) Do model species differ in wing shape? (2) Do *P. dardanus* females that mimic different model species differ in wing shape? (3) Is there a correspondence between wing shapes of models and mimics? (4) In *P. dardanus*, is there sexual dimorphism in wing shapes when hind wing tails are excluded?

Methods

Species and specimens

Five model species were examined: *Amauris echeria*, *Amauris niavius*, *Danaus chrysippus* (Nymphalidae, Danainae, Danaini), *Acraea jodutta*, and *Acraea poggei* (Nymphalidae, Heliconiinae, Acraeini) (Fig. 1). Each of these species is a model for one of the five mimetic color forms of *P. dardanus* analyzed in this study.

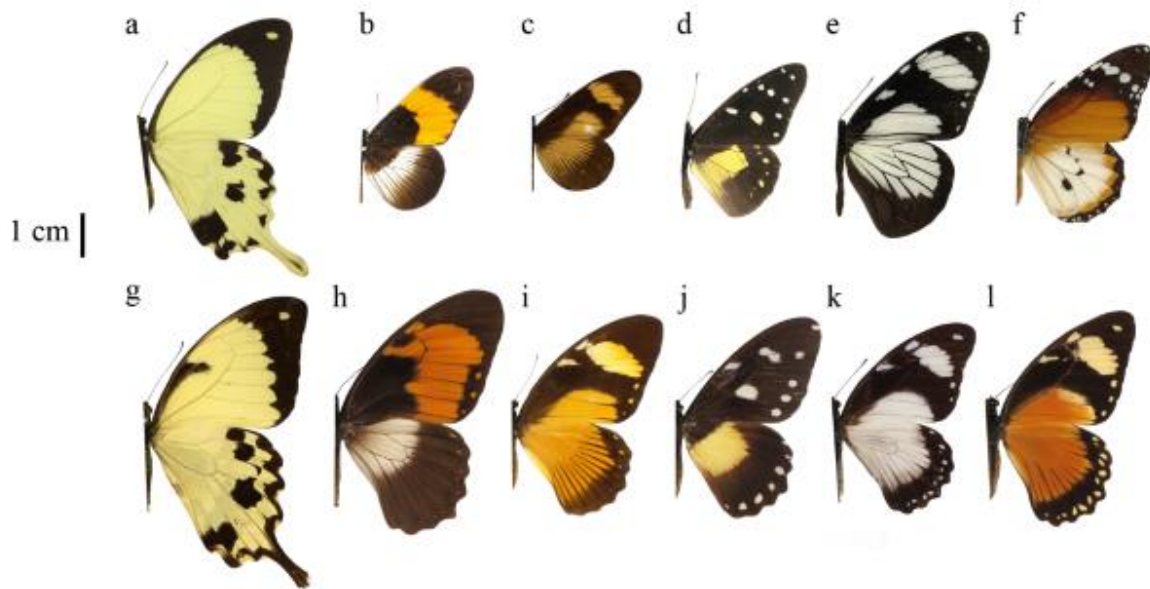


Figure 1: *Papilio dardanus* and its mimicy models: **a**, *P. dardanus* male; **b**, *Acraea poggei*; **c**, *Acraea jodutta*; **d**, *Amauris echeria*; **e**, *Amauris niavius*; **f**, *Danaus chrysippus*; **g**, *P. dardanus* male-like female; **h**, *P. dardanus* f. *planemoides*; **i**, *P. dardanus* f. *niobe*; **j**, *P. dardanus* f. *cenea*; **k**, *P. dardanus* f. *hippocoon*; **l**, *P. dardanus* f. *trophonius*.

We examined six female *P. dardanus* color forms, f. *cenea*, f. *hippocoon*, f. *trophonius*, f. *niobe*, f. *planemoides*, and male-like, which were categorized according to Thompson's (2014) descriptions of *P. dardanus* phenotypic diversity (Fig. 1). Although some female mimetic forms have hind wing tails (see Thompson 2014), these were not examined here. Female color forms

were represented by individuals from throughout the five polymorphic mainland subspecies (Table S1).

We used a recent phylogeny (Zakharov et al., 2004) to select four non-mimetic *Papilio* species as a baseline to evaluate wing shape differences between the sexes not attributable to female-limited mimicry. Figure 2 illustrates males and females of two species within the *P. dardanus* clade (*P. constantinus*, *P. delalandei*) and two from a sister clade (*P. troilus*, *P. cresphontes*) examined here.

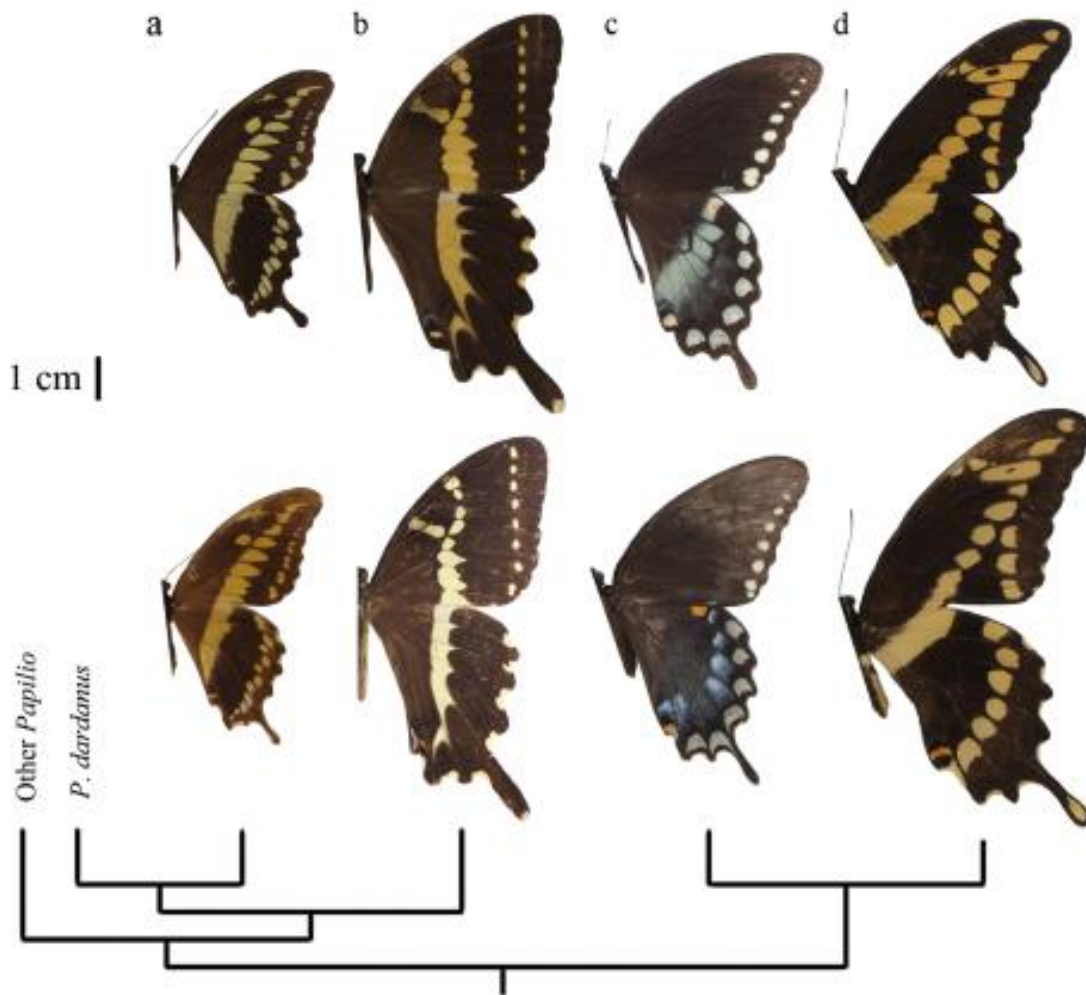


Figure 2: Four species used as a baseline to evaluate wing shape differences between sexes in non-mimetic *Papilio*: **a**, *P. constantinus*; **b**, *P. delalandei*; **c**, *P. troilus*; **d**, *P. cresphontes*. Males shown above females. The phylogenetic relationships between *P. dardanus* and these four non-mimetic congeners are indicated below the images (following Zakharov et al., 2004).

A total of 167 pinned museum specimens were used for morphometric analysis of wing shape (see Table S1 for sample sizes and locality data). Only specimens with intact bodies (for sex determination) and at least one intact forewing and hind wing were used.

Image processing

Specimens were photographed using a Canon Powershot SX40HS mounted on a tripod such that the camera sensor was in the same horizontal plane as the butterfly wings. Pinned butterflies were positioned on a flat surface such that the exposed wing was displayed perpendicular to the view of the camera. Only images in which the wings were laid flat along the surface and were not obstructed by the abdomen were used for analyses.

Wing outlines were obtained by cropping images in Photoshop to isolate each focal wing from the rest of the specimen. For analysis of hind wing sexual dimorphism in *Papilio* species, the hind wing tails were removed in Photoshop (Fig. 3) such that the wing outline formed a scalloped pattern similar to that of naturally tail-less papilionids (e.g., *Battus polydamas*). This enabled comparisons of overall hind wing shape that were not affected by the presence or absence of a tail.



Figure 3: Outline of a *P. dardanus* male forewing whose tail (grey) was cropped, leaving a tailless wing (white).

Analyses

We quantified wing shape variation among model species, *P. dardanus* males and female color forms, and non-mimetic *Papilio* species. The software package SHAPE 1.3 (Iwata & Ukai 2002) was used to create Elliptical Fourier descriptors (EFD's), which analyze variation in complete shape outline rather than at discrete homologous points. This method was preferred because homologous landmark points determined by wing venation were not comparable between papilionid and nymphalid butterflies due to phylogenetic differences in venation patterns. Importantly, SHAPE is capable of recognizing subtle differences in whole-outline variation that may not be detected by a fixed set of discrete venation-based landmarks (e.g., the scalloping of the hind wing edge). We used twenty harmonics to create the EFD's, which were standardized for size and positioned such that forewing inner margin and hind wing costal margin were horizontally aligned.

To quantify wing shape differences between specimens, variation in wing outline was reduced to several effective principal components (proportion of variation explained > 1/total number of PC's). Visualizations of the two most informative principal components (PC1 and PC2) were reconstructed to display both extremes of the variation encapsulated by that component. Individual specimens were then plotted using the Eigenvalues for PC1 and PC2 to look for clustering by species or color morph. MANOVA was used to test the significance of such clusters, with Eigenvalues for PC1 and PC2 used as dependent variables. PC3 was included only in the analysis of *P. dardanus* hind wings, where PC1 and PC2 collectively described less than 50% of total variation. Pair-wise MANOVA with the Bonferroni correction for multiple comparisons was used to identify species or color morphs that separated significantly from other groups.

Results

Wing shape differences among models

As the model species belong to separate subfamilies within the Nymphalidae, their wing shapes were anticipated to differ. Variation in forewing shape among the five model species is shown in Fig. 4a. PC1 accounted for 66% of the total forewing variation, primarily in the length of the forewing inner margin and the shape of the apex (rounded or pointed). PC2 explained 14% of the variation, and corresponded to the projection of the wing apex. The three Danaini models showed some overlap in shape space, with no apparent clustering by sex. The two Acraeini models were separated from Danaini, with sexual dimorphism apparent only in *Acraea poggei*. A MANOVA analysis indicated that forewing shape differs significantly between the five model species ($p < 0.001$ after Bonferroni correction) and also between the Acraeini and Danaini groups ($p < 0.001$ after Bonferroni correction, Table S2).

Hind wing shape variation in the models was similar to that in the forewing (Fig. 4b). In this case, PC1 and PC2 accounted for 31 and 28 % of total variation and broadly described overall wing roundness. Within Danaini, *Danaus chrisippus* and *Amauris echeria* clustered together,

but *Amauris niavius* was separated from them along the PC2 axis. The Acraeini clustered together in a distinct area of shape space from that occupied by the Danaini. As with the forewings, hind wing shape differed significantly between the five model species (MANOVA, $p < 0.001$ after Bonferroni correction, Table S2) and also between the Acraeini and Danaini groups (MANOVA, $p < 0.001$ after Bonferroni correction, Table S2). Given wing shape differences in the models, we also expected the various *P. dardanus* mimics to differ in wing shape.

Wing shape differences in P. dardanus females

As female *P. dardanus* color forms match those of models that vary in wing shape, we tested if these mimetic forms showed distinctive wing shapes. Forewing shape variation among the mimetic and male-like *P. dardanus* females is shown in Fig. 5a. PC1 and PC2 described 32 and 28% of the variation, which involves the projection of the wing apex resulting in a slightly concave outer margin. Although the PC1-PC2 plot showed that the *P. dardanus* female forms overlap in shape space, MANOVA uncovered significant differences when all forms were considered together ($p < 0.001$, Table S2). Form *cenea* differed from f. *hippocoön* ($p = 0.029$) and male-like females ($p = 0.023$ after Bonferroni correction, Table S3) in a pairwise MANOVA, but others did not.

Figure 5b shows hind wing shape variation among mimetic *P. dardanus* females. PC1, PC2, and PC3 accounted for 34%, 15%, and 12% of the variation, and described the outer margin scalloping as well as curvature of the costal and inner margins. As with the forewings, there were significant differences in hind wing shape when all forms were analyzed together despite overlap in shape space (MANOVA, $p < 0.01$, Table S2). Again, only f. *cenea* and f. *hippocoön* differed significantly in a pairwise MANOVA ($p < 0.01$ after Bonferroni correction, Table S3).

Wing shape association between models and mimics

Given wing shape differences among *P. dardanus* female color forms, and f. *cenea* and f. *hippocoön* in particular, we investigated the potential for wing shape correspondence between mimics and models. Forewing shapes of mimics differed significantly from their Danaini and Acraeini models (MANOVA, $p < 0.001$, Table S2; Fig. 6a). Mimics partly overlapped in shape space with *Amauris niavius*, but this model species was not associated exclusively with its mimic, f. *hippocoön*. Hind wing shapes of mimics and models differed significantly (MANOVA, $p < 0.001$, Table S2) where PC1 showed separation of the groups (Fig. 6b).

Wing shape sexual dimorphism in P. dardanus

We looked for wing shape sexual dimorphism within *P. dardanus* and four congeneric non-mimetic species. Males and females of the four non-mimetic *Papilio* species did not differ in forewing or hind wing shape (Fig. 7a, b, Table S2). In *P. dardanus*, forewing shape did not differ between sexes (Fig. 7a), but hind wings of mimetic females differed significantly from males (Fig. 7b; pairwise MANOVA, $p < 0.001$ after Bonferroni correction, Table S2). Moreover, *P. dardanus* male-like females generally clustered with conspecific males along PC1 due to differences in curvature of the hind wing margins.

While sexual dimorphism was evident only in *P. dardanus*, the five model species varied significantly in both forewing (MANOVA, $p < 0.01$, Table S2) and hind wing shape (MANOVA, $p < 0.01$, Table S2).

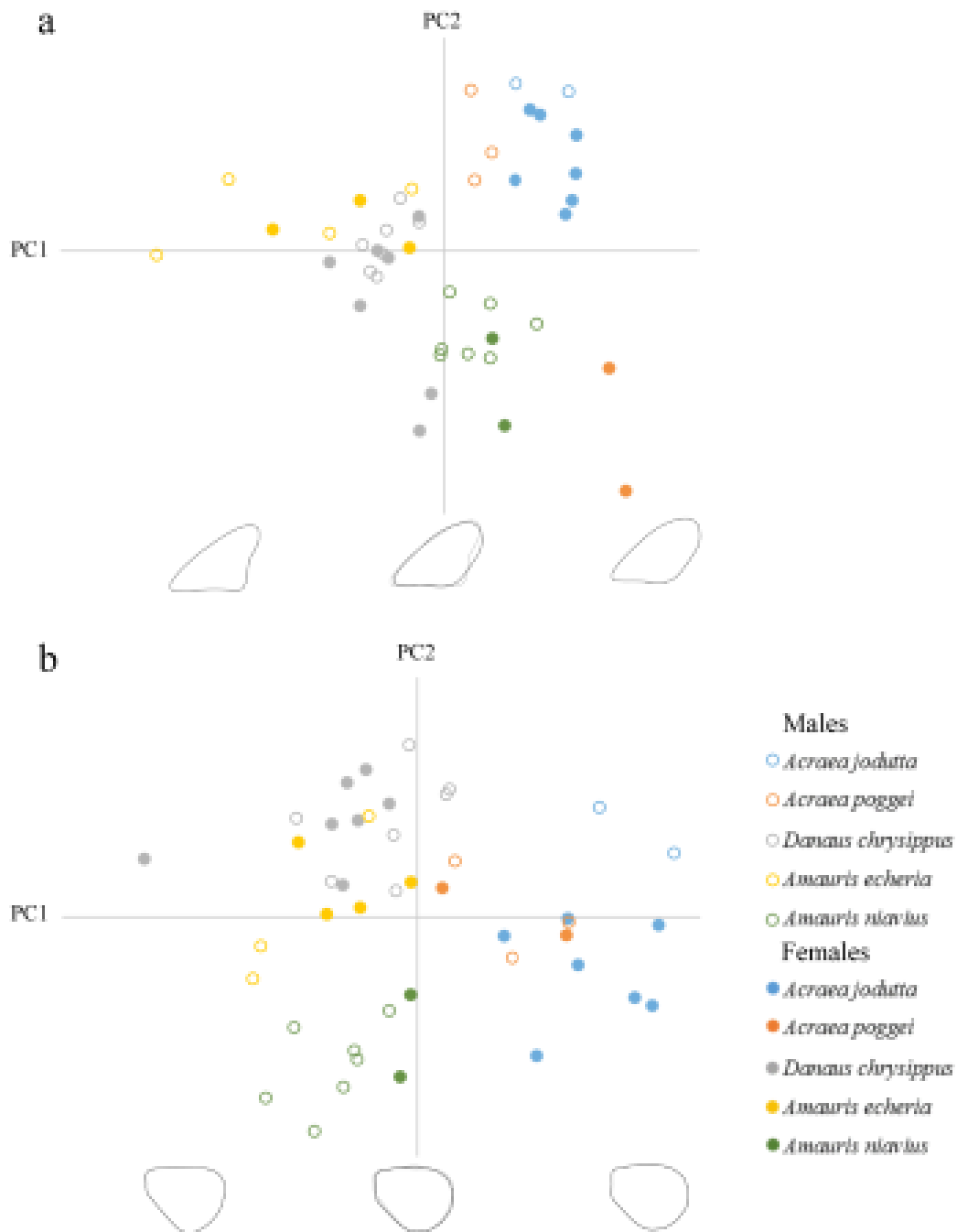


Figure 4: Principal components plots comparing individuals of the five model species: **a**, forewings; **b**, hind wings. Wing outlines below each plot represent the most extreme variants within PC1, with a superimposition of both in the center.

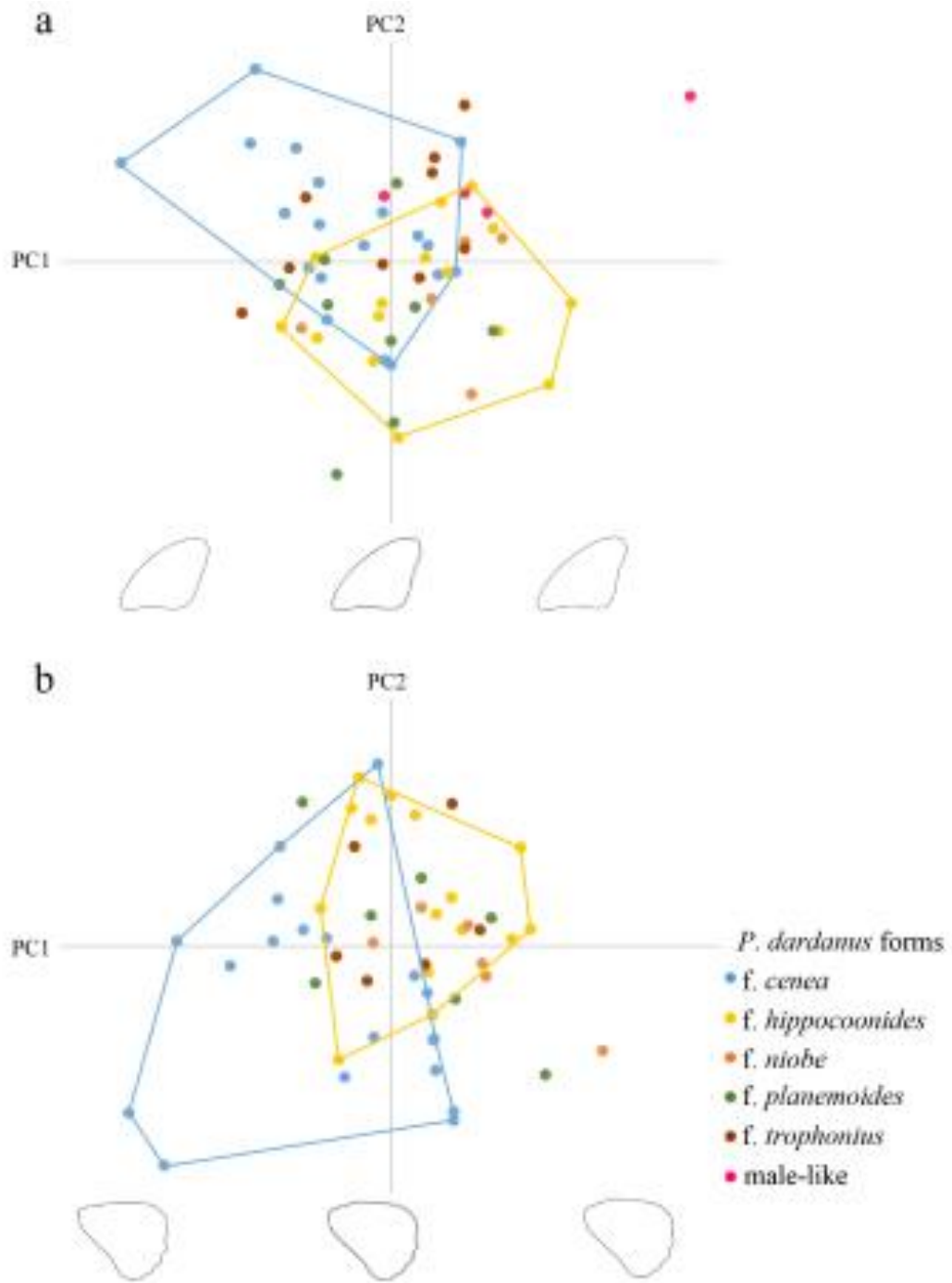


Figure 5: Principal components plots comparing *P. dardanus* mimetic and male-like females: **a**, forewings; **b**, hind wings. Polygons delineate shape space covered by forms *cenea* (blue) and *hippocoon* (yellow). Wing outlines below each plot represent the most extreme variants within PC1, with a superimposition of both in the center.

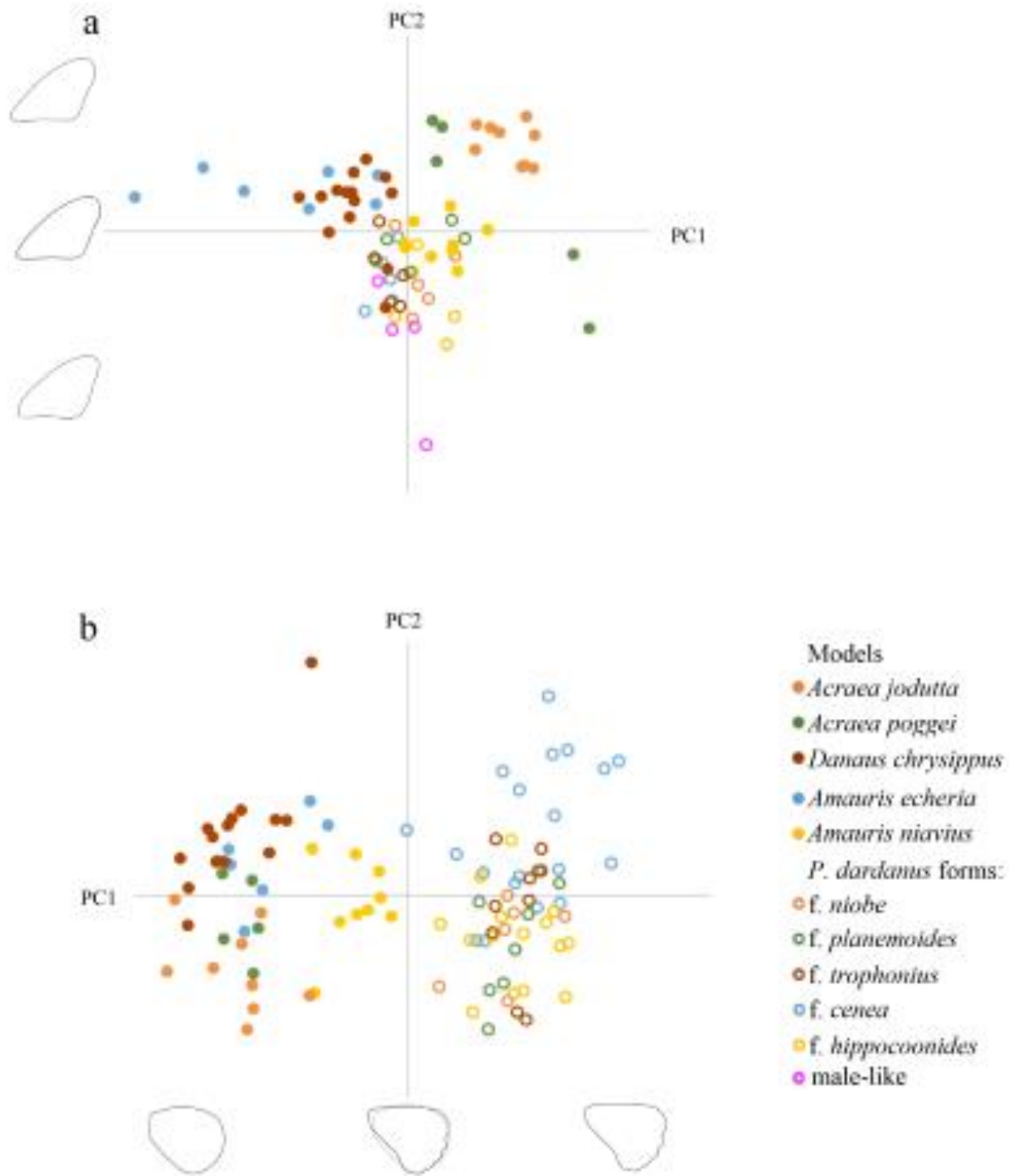


Figure 6: Principal components plots comparing *P. dardanus* mimetic and male-like females to the models: **a**, forewings, note that models and mimics are separated along the PC2 axis; **b**, hind wings. Wing outlines on the left of the forewing plot (PC2) and below the hind wing plot (PC1) represent the most extreme variants, with a superimposition of both in the center.

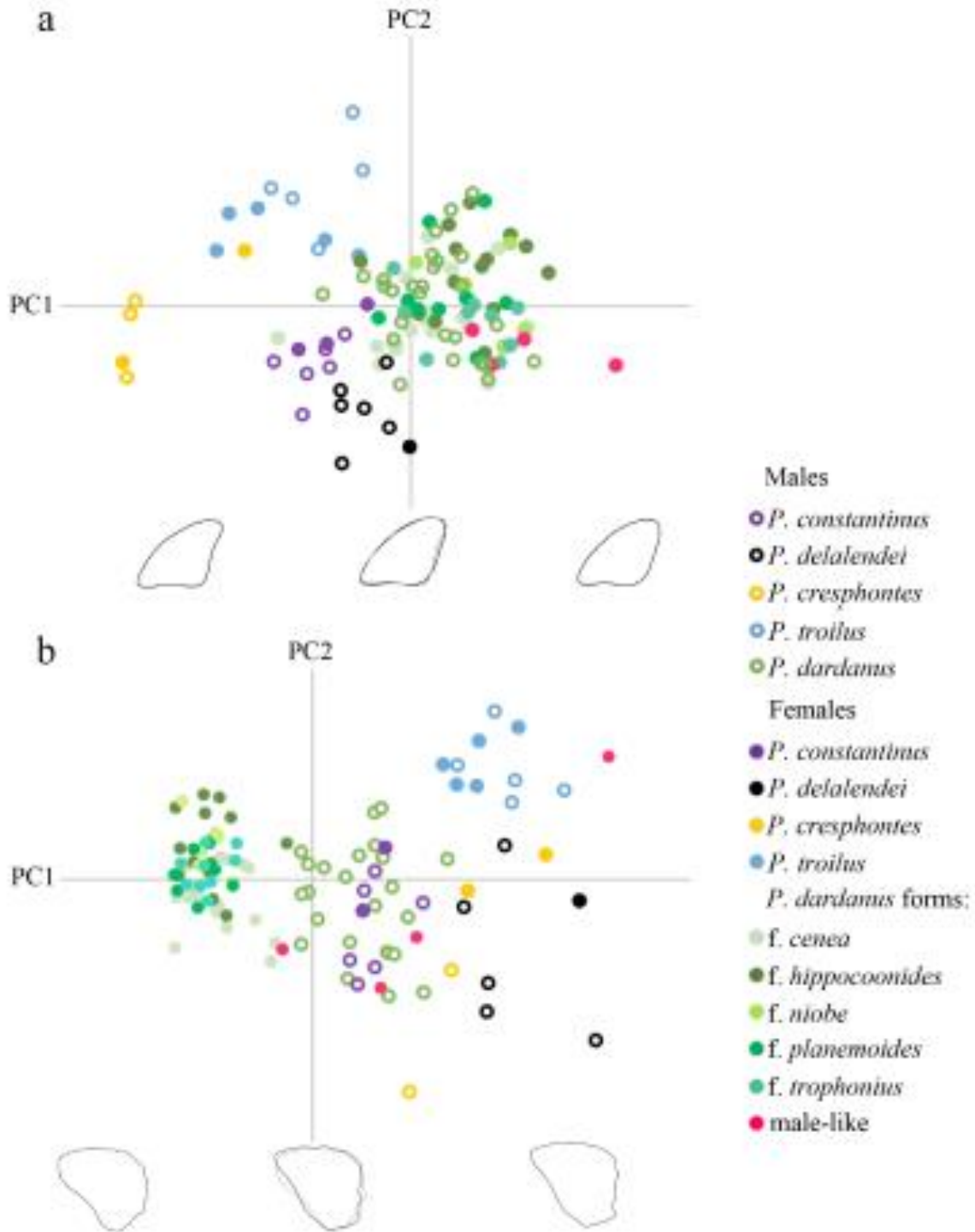


Figure 7: Principal components plots comparing males and females of *P. dardanus* and four non-mimetic *Papilio* species: **a**, forewings; **b**, hind wings. Wing outlines represent the most extreme variants within PC1, with a superimposition of both in the center.

Papilio constantinus and *P. delalandei* belong to the same clade as *P. dardanus*, and these species were most closely associated to *P. dardanus* in both forewing and hind wing shape space (Fig. 2, 7a, b). *Papilio troilus* and *P. cresphontes* belong to a more distant clade within *Papilio* (Fig. 2), and separated more clearly from *P. dardanus* (Fig. 7a, b).

Discussion

This study investigated whether mimetic *P. dardanus* females showed wing shape convergence with their unpalatable models. Differences among model species were statistically significant and clearly distinguishable on PCA plots of forewing and hind wing variation (Fig. 4). Danaini and Acraeini taxa differed in wing shape, and a primary source of variation among model species was the relative length of the forewing inner margin and the angle of the tornus. Differences in wing morphology of the model species, and ultimately their flight pattern, can be therefore considered possible signals for mimicry by the various *P. dardanus* female color forms.

Wing shape can evolve to optimize color pattern visibility (Outomuro et al., 2013) and might influence flight pattern (Betts & Wootton, 1988; Dudley, 1990). In concert, wing and body structure (e.g., mass allocation to thorax) have been shown to affect components of butterfly flight such as speed, wing-beat frequency, and body-pitching frequency, suggesting that convergence in wing shape could help promote similarity of flight patterns between Batesian mimics and models, or Mullerian comimics (Dudley & Srygley, 1994; Srygley, 1994, 1999). For example, given their distant phylogenetic position within Nymphalidae (Wahlberg et al., 2009), the Heliconiini and Ithomiini have similar wing and body allometry that can be considered convergent at a macroevolutionary level (Strauss, 1990). Therefore, selection operating on cross-tribe comimics could further refine their similarity in both wing color pattern and wing shape. Based on this premise, the analyses by Jones et al. (2013) examined wing shape variation in three color forms of the locally polymorphic *Heliconius numata* and their *Melinaea* Mullerian comimics, but only found wing shape convergence between *H. numata* f. *silvana* and *M. ludovica ludovica*. These authors nonetheless concluded that shape convergence between these taxa might have an adaptive influence on flight characteristics to complement their wing color pattern similarity.

We found that forewing and hind wing shape varied significantly among the five mimetic *P. dardanus* color forms (Fig. 5a, b). The variation was nonetheless driven by differences between f. *cenea* and f. *hippocoön*. Interestingly, f. *cenea* is distinct not only in wing shape, it is also the most unique mimetic color pattern. Forewing color pattern is restricted to small spots overlain by extensive black markings, whereas all other color forms show distal color bands with limited black markings (Fig. 1). Assuming that the *P. phorcas* pattern is ancestral to that of *P. dardanus*, Nijhout (2003) hypothesized that a mutation of large effect could have produced a *hippocoön*-like phenotype, and described a scenario by which f. *cenea* could have evolved from f. *hippocoön*. Although the genetic control of wing shape has not been investigated in *P. dardanus*, our observation that the greatest disparity in wing shape corresponds to these putative ancestral and derived color forms (as per Nijhout, 2003) warrants further investigation.

Although *P. dardanus* forewings showed shape variation among mimetic color forms, we found no correlation between female mimics and their corresponding models. The forewing is somewhat triangular and has a produced apex in both *P. dardanus* and the Danaini models (Figs 1, 6a), but this overall shape cannot be attributed to mimetic convergence. Unlike many unpalatable species, *Danaus* and *Amauris* can be considered strong fliers (Pinheiro et al. 2016; PJD and CMP pers. obs.), and their produced forewing apex likely increases lift during flight (e.g., Berwaerts et al. 2002, 2006; see also Dudley, 2002). As species of *Papilio* are also strong fliers, their wing architecture would be expected to increase lift as well. Therefore, the overall forewing similarity between Danaini and *Papilio dardanus* (Figs 1, 6a) is likely due to their similar flight demands. In contrast, in Acraeini models the distance between the forewing base and tornus is reduced along the inner margin. This forewing shape is also found in chemically protected, slow flying Ithomiini and Heliconiini butterflies (Strauss, 1990), and observations on African Acraeini indicate that their flight is slower and less maneuverable than sympatric Danaini (PJD pers. obs.). Predictably, female *P. dardanus* forewings clearly separate in shape space from those of their Acraeini models (Fig. 6a). From a behavioral standpoint, shape convergence of female *P. dardanus* onto these models would entail morphological changes that are expected to affect flight performance, perhaps making them more vulnerable to predation. Moreover, it would require the evolution of a wing development pathway linked to the *H* locus alleles that determine the specific color resemblance to Acraeini models (see Jones et al., 2013 for a similar line of reasoning).

Hind wing shape convergence of mimetic *P. dardanus* female forms onto their models is primarily achieved by the loss of hind wing tails. However, two aspects of hind wing shape clearly differentiate mimetic *P. dardanus* females from their models: the outer margin is scalloped, and the inner margin is straight or arched (Figs 1, 6b). These attributes were found in all individuals (male and female) of *P. dardanus* as well as the other *Papilio* species. As such, selection for more accurate hind wing mimicry might be restricted by factors such as cross-sex genetic covariance that could limit wing shape sexual dimorphism in this genus (see Poissant et al., 2010). Nonetheless, the artificial exclusion of tails from *P. dardanus* males and male-like females, and also both sexes of four non-mimetic *Papilio* species, allowed us to explore sex-related hind wing shape variation in further detail. Even when tails were excluded, mimetic *P. dardanus* female forms still clustered apart from conspecific male-like females, conspecific males, and both sexes of *P. constantinus*, *delalandei*, *cresphontes* and *troilus* (Fig. 7b). Importantly, we found no evidence of hind wing shape sexual dimorphism in the non-mimetic *Papilio* species (Fig. 7b), reinforcing the idea that mimicry is driving hind wing shape changes in *P. dardanus* females beyond a simple loss of the tail. Hind wing tail development is known to be genetically controlled in *P. dardanus* (Clarke & Sheppard, 1960d), and the same allele that leads to tail loss might also have an effect on the hind wing margin surrounding vein M_3 where the tail is located. Although this was not empirically examined here, forewings are more important in powering flight (Jantzen & Eisner, 2008) so the loss of hind wing tails and associated modifications on the wing margin could considerably improve female *P. dardanus* mimetic resemblance to Danaini and Acraeini models with minimal effects on their flight pattern. Interestingly, female-limited mimicry in *Papilio polytes alphenor* also involves hind wing modifications, but in their case mimetic convergence on *Pachliopta aristolochiae* requires the

development of a tail (Clarke & Sheppard, 1972; Kunte et al., 2014). In *P. polytes*, both wing color pattern and hind wing tail presence are controlled by *doublesex* (Kunte et al., 2014), a genetic mechanism that differs from that employed by *P. dardanus* (e.g. Timmermans et al., 2014; Clark et al., 2008).

Bird predators can recognize flight patterns (Chai, 1986, 1990) and might be able to discriminate wing shape (see Kazemi et al., 2014). Given that flight pattern and wing shape are associated to some degree, one can ask: what prevents wing shape convergence in the *P. dardanus* female forms? Considering its size and colors, female *P. dardanus* mimetic color signal should be easily perceived by birds, and as a palatable butterfly it should benefit from using escape flight as a defense against predation. Batesian mimics that converge on the slow flight behavior of their chemically defended models incur a predation risk, and some species shift from slow, deliberate flight, to fast, erratic flight upon predatory pursuit (Srygley & Chai, 1990). To do this, such species must exhibit a suite of body and wing characteristics that in concert allow for fast, maneuverable flight (Marden & Chai, 1991; Srygley & Dudley 1993). Escape flight is known to be an effective defense for palatable and unpalatable species alike, and both might use bright wing color patterns to advertise their escape abilities (Pinheiro & Freitas, 2014; Pinheiro et al., 2016). Despite being a well-known and widespread species, there are apparently no published field observations on flight behaviors in *P. dardanus* females, and such observations are required to assess their ability to evade aerial pursuit by predators. Phylogenetic constraints on essential flight behaviors may also be restricting mimetic convergence of *P. dardanus* forewing shape. For instance, *Papilio* butterflies typically flutter as they feed, a behavior that has been suggested to increase nectar access relative to competitors by expediting movement from flower to flower (Stone et al., 1988). Moreover, female swallowtails use flight when assessing host plants, and flutter when ovipositing. Altering forewing shape might compromise the performance of these behaviors. It is therefore possible that the female *P. dardanus* wings retain the architecture needed for flight behaviors common among *Papilio* species at the expense of wing shape mimicry and associated flight pattern signals.

Our analyses show that wing shape modifications associated with female-limited mimicry in *P. dardanus* are centered on the hind wing. This suggests that hind wings are evolving independently from the forewings in this species, which was also found to be the case in *Morpho* butterflies (Chazot et al., 2016) and *Calopteryx* damselflies (Outomuro et al., 2012). We hypothesize that opposing selective pressures might be operating on wing morphology; i.e., preserving flight behaviors that have an important role in their natural history *versus* improving mimetic convergence. Female-limited, locally polymorphic mimicry in *P. dardanus* captivated multiple generations of researchers, and genetic basis of color convergence is well understood. Time is ripe for field studies that focus on their flight behavior, local predator interactions, and population biology.

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Appendix

Species (n)	Sex	Color Form	Subspecies	Country	City/ Region	Museum
<i>Acraea jodutta</i>	F			Uganda	Kemengo Forest	CMNH
(7 F, 2 M)	F			Uganda	Kemengo Forest	CMNH
	F			Uganda	Bufumbo Forest	CMNH
	F			Unknown	Unknown	CMNH
	F			Uganda	Kemengo Forest	CMNH
	F			Uganda	Entebbe	NMNH
	F			Uganda	Entebbe	NMNH
	M			Uganda	Budongo Forest	CMNH
	M			Uganda	Kayonza Kigezi	NMNH
<i>Acraea poggei</i>	F			Uganda	Masaka	CMNH
(2 F, 3 M)	F			Uganda	Entebbe	NMNH
	M			Unknown	Unknown	CMNH
	M			Unknown	Unknown	CMNH
	M			Uganda	Masaka	NMNH
<i>Amauris echeria</i>	F			Uganda	Budongo Forest	CMNH
(3 F, 5 M)	F			Kenya	Kakamega	LACM
	F			S. Africa	Natal Margate	LACM
	M			Uganda	Kigezi	CMNH
	M			Kenya	Kakamega	LACM
	M			S. Africa	Natal Izokha	LACM
	M			Kenya	Kakamayo	NMNH
	M			Kenya	Nemanga	NMNH
<i>Amauris niavius</i>	F			Kenya	Diani	CMNH
(2 F, 7M)	F			Kenya	Diani	CMNH
	M			Unknown	Unknown	CMNH
	M			Kenya	Diani	CMNH
	M			Unknown	Unknown	LACM
	M			Sierra Leone	Freetown	LACM
	M			Kenya	Noko Forest	LACM
	M			Unknown	Unknown	LACM
	M			Cameroon	Bitye	NMNH
<i>Danaus chrysippus</i>	F			Cameroon	Elat	CMNH
(7 F, 7 M)	F			Unknown	Unknown	CMNH
	F			Liberia	Unknown	CMNH
	F			S. Africa	Boni Forest	LACM
	F			Nigeria	Kaduna	LACM
	F			Kenya	Nairobi	LACM
	F			Unknown	Unknown	LACM

	M			Unknown	Unknown	CMNH
	M			S. Africa	Durban	LACM
	M			Unknown	Unknown	LACM
	M			Unknown	Unknown	LACM
	M			Kenya	Boni Forest	LACM
	M			Uganda	Kakindo	NMNH
	M			Kenya	Unknown	NMNH
<i>Papilio constantinus</i>	F			S. Africa	Unknown	CMNH
(3 F, 6 M)	F			Malawi	Unknown	CMNH
	F			Zimbabwe	Victoria Falls	NMNH
	M			Somalia	Unknown	CMNH
	M			Kenya	Unknown	CMNH
	M			Unknown	Unknown	CMNH
	M			Unknown	Unknown	CMNH
	M			Kenya	Kibwezi	NMNH
	M			S. Africa	Neslspruit	NMNH
<i>Papilio cresphontes</i>	F			USA	New Orleans	UNO
(2 F, 4 M)	F			USA	New Orleans	UNO
	M			USA	New Orleans	UNO
	M			USA	New Orleans	UNO
	M			USA	New Orleans	UNO
	M			USA	New Orleans	UNO
<i>Papilio dardanus</i>	F	<i>cenea</i>	<i>cenea</i>	S. Africa	Durban	LACM
(21 F f. <i>cenea</i>)	F	<i>cenea</i>	<i>cenea</i>	S. Africa	Durban	LACM
	F	<i>cenea</i>	<i>cenea</i>	S. Africa	Natal	CMNH
	F	<i>cenea</i>	<i>cenea</i>	S. Africa	Natal	CMNH
	F	<i>cenea</i>	<i>cenea</i>	S. Africa	Natal	CMNH
	F	<i>cenea</i>	<i>dardanus</i>	Uganda	Ituri Forest	NMNH
	F	<i>cenea</i>	<i>dardanus</i>	Uganda	Ituri Forest	NMNH
	F	<i>cenea</i>	<i>flavicornis</i>	Kenya	Mt. Kulal	CMNH
	F	<i>cenea</i>	<i>flavicornis</i>	Kenya	Mt. Kulal	CMNH
	F	<i>cenea</i>	<i>flavicornis</i>	Kenya	Mt. Kulal	CMNH
	F	<i>cenea</i>	<i>meseres</i>	Uganda	Mabira Forest	NMNH
	F	<i>cenea</i>	<i>ochraceana</i>	C.A.R.	Unknown	LACM
	F	<i>cenea</i>	<i>ochraceana</i>	Kenya	Lake Paradise	LACM
	F	<i>cenea</i>	<i>ochraceana</i>	Kenya	Lake Paradise	LACM
	F	<i>cenea</i>	<i>ochraceana</i>	Kenya	Mt. Marsabit	CMNH
	F	<i>cenea</i>	<i>ochraceana</i>	Kenya	Mt. Marsabit	CMNH
	F	<i>cenea</i>	<i>ochraceana</i>	Kenya	Mt. Marsabit	CMNH
	F	<i>cenea</i>	<i>polytrophus</i>	Kenya	Nairobi	CMNH
	F	<i>cenea</i>	<i>polytrophus</i>	Kenya	Ngong	CMNH

	F	<i>cenea</i>	<i>tibullus</i>	Kenya	Nyeri	NMNH
	F	<i>cenea</i>	unknown	Unknown	Unknown	LACM
<i>Papilio dardanus</i>	F	<i>hippocoon</i>	<i>cenea</i>	S. Africa	Durban	LACM
(14 F f. <i>hippocoon</i>)	F	<i>hippocoon</i>	<i>cenea</i>	S. Africa	East Transvaal	NMNH
	F	<i>hippocoon</i>	<i>dardanus</i>	Cameroon	Elat	CMNH
	F	<i>hippocoon</i>	<i>dardanus</i>	Cameroon	Lolodorf	CMNH
	F	<i>hippocoon</i>	<i>dardanus</i>	Congo	Unknown	LACM
	F	<i>hippocoon</i>	<i>dardanus</i>	Ivory Coast	Abidjan	NMNH
	F	<i>hippocoon</i>	<i>dardanus</i>	Unknown	Bule Country	CMNH
	F	<i>hippocoon</i>	<i>meseres</i>	Uganda	Bugoma Forest	LACM
	F	<i>hippocoon</i>	<i>tibullus</i>	Malawi	Cholo	CMNH
	F	<i>hippocoon</i>	<i>tibullus</i>	Malawi	Luchenza	CMNH
	F	<i>hippocoon</i>	<i>tibullus</i>	Malawi	Mombasa	CMNH
	F	<i>hippocoon</i>	<i>tibullus</i>	S. Africa	Natal	CMNH
	F	<i>hippocoon</i>	<i>tibullus</i>	Zimbabwe	Mutare	NMNH
	F	<i>hippocoon</i>	unknown	Unknown	Unknown	CMNH
<i>Papilio dardanus</i>	F	<i>niobe</i>	<i>dardanus</i>	Unknown	Unknown	LACM
(6 F f. <i>niobe</i>)	F	<i>niobe</i>	<i>dardanus</i>	Unknown	Unknown	NMNH
	F	<i>niobe</i>	<i>meseres</i>	Uganda	Kampala	NMNH
	F	<i>niobe</i>	<i>meseres</i>	Uganda	Mabira Forest	NMNH
	F	<i>niobe</i>	<i>tibullus</i>	Kenya	Mombasa	CMNH
	F	<i>niobe</i>	unknown	Unknown	Unknown	CMNH
<i>Papilio dardanus</i>	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Bufumbo	CMNH
(9 F f. <i>planemoides</i>)	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Entebbe	CMNH
	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Entebbe	CMNH
	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Kampala	NMNH
	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Kemengo	CMNH
	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Mabira Forest	NMNH
	F	<i>planemoides</i>	<i>meseres</i>	Uganda	Mabira Forest	NMNH
	F	<i>planemoides</i>	unknown	Unknown	Unknown	NMNH
	F	<i>planemoides</i>	unknown	Unknown	Unknown	NMNH
<i>Papilio dardanus</i>	F	<i>trophonius</i>	<i>cenea</i>	S. Africa	Transvaal	CMNH
(9 F f. <i>trophonius</i>)	F	<i>trophonius</i>	<i>cenea</i>	S. Africa	Unknown	LACM
	F	<i>trophonius</i>	<i>dardanus</i>	Congo	Ogoue	CMNH
	F	<i>trophonius</i>	<i>dardanus</i>	Uganda	Ituri Forest	NMNH
	F	<i>trophonius</i>	<i>polytrophus</i>	Kenya	Ngong	CMNH
	F	<i>trophonius</i>	<i>polytrophus</i>	Kenya	Ngong	CMNH
	F	<i>trophonius</i>	<i>polytrophus</i>	Kenya	Ngong	CMNH
	F	<i>trophonius</i>	<i>polytrophus</i>	Kenya	Ngong	CMNH
	F	<i>trophonius</i>	unknown	Unknown	Unknown	CMNH
<i>Papilio dardanus</i>	F	male-like	<i>antinorii</i>	Ethiopia	Adola	NMNH

(4 F male-like)	F	male-like	<i>meriones</i>	Madagascar	Delacour	NMNH
	F	male-like	<i>meriones</i>	Madagascar	Unknown	CMNH
	F	male-like	<i>meriones</i>	Madagascar	Unknown	NMNH
<i>Papilio dardanus</i>	M		<i>antinorii</i>	Unknown	Unknown	NMNH
(27 M)	M		<i>cenea</i>	S. Africa	Durban	LACM
	M		<i>cenea</i>	S. Africa	Unknown	LACM
	M		<i>cenea</i>	S. Africa	Unknown	LACM
	M		<i>cenea</i>	Unknown	Unknown	LACM
	M		<i>dardanus</i>	C.A.R.	Bangui	NMNH
	M		<i>dardanus</i>	C.A.R.	Unknown	LACM
	M		<i>dardanus</i>	Cameroon	Lolodorf	CMNH
	M		<i>dardanus</i>	Cameroon	Lolodorf	CMNH
	M		<i>dardanus</i>	Cameroon	Nanga Eboko	LACM
	M		<i>dardanus</i>	Unknown	Unknown	CMNH
	M		<i>meriones</i>	Madagascar	Mananjary	LACM
	M		<i>meriones</i>	Madagascar	Maromandia	CMNH
	M		<i>meriones</i>	Madagascar	Unknown	NMNH
	M		<i>meriones</i>	Madagascar	Unknown	NMNH
	M		<i>meseres</i>	Uganda	Budongo Forest	LACM
	M		<i>meseres</i>	Uganda	Bugoma Forest	LACM
	M		<i>meseres</i>	Uganda	Mpanga Forest	NMNH
	M		<i>polytrophus</i>	Kenya	Nairobi	LACM
	M		<i>polytrophus</i>	Kenya	Nairobi	NMNH
	M		<i>polytrophus</i>	Uganda	Ituri Forest	NMNH
	M		<i>tibullus</i>	Kenya	Mombasa	CMNH
	M		<i>tibullus</i>	Kenya	Mombasa	CMNH
	M		<i>tibullus</i>	Kenya	Nairobi	LACM
	M		<i>tibullus</i>	Kenya	Unknown	LACM
	M		<i>tibullus</i>	Unknown	Unknown	NMNH
	M		unknown	Unknown	Unknown	NMNH
<i>Papilio delalandei</i>	F			Madagascar	Unknown	CMNH
(1 F, 6M)	M			Madagascar	Unknown	CMNH
	M			Madagascar	Unknown	CMNH
	M			Madagascar	Unknown	CMNH
	M			Madagascar	Unknown	CMNH
	M			Madagascar	Unknown	CMNH
	M			Madagascar	Unknown	LACM
<i>Papilio troilus</i>	F			USA	New Orleans	UNO
(5 F, 5 M)	F			USA	New Orleans	UNO
	F			USA	New Orleans	UNO
	F			USA	New Orleans	UNO

F	USA	New Orleans	UNO
M	USA	New Orleans	UNO
M	USA	New Orleans	UNO
M	USA	New Orleans	UNO
M	USA	New Orleans	UNO
M	USA	New Orleans	UNO

Table S1: Specimens used in this study. Abbreviations: F, female; M, male; CMNH, Carnegie Museum of Natural History; LACM, Natural History Museum of Los Angeles County; NMNH, National Museum of Natural History (Smithsonian Institution); UNO, University of New Orleans.

Test	Df	Pillai	approx F number	numerator df	denominator df	Pr(>F)	
model species fw	4	1.0998	11.302	8	74	2.604E-10	**
model species hw	4	1.4991	29.18	8	78	2.20E-16	**
model tribes fw	1	0.7234	53.615	2	41	3.61E-12	**
model tribes hw	1	0.77863	68.589	2	39	1.70E-13	**
female mimics fw	1	0.7234	53.615	2	41	3.61E-12	**
female mimics hw	4	0.43552	2.1653	12	153	0.01597	*
models x mimics fw	1	0.41534	23.444	2	66	2.03E-08	**
models x mimics hw	1	0.098973	5.3824	2	98	0.006056	**
<i>Papilio</i> species fw	4	1.1755	40.629	8	228	2.20E-16	**
<i>Papilio</i> species hw	4	0.93045	24.793	8	228	2.20E-16	**
<i>onstantinus</i> fw sex	1	0.33561	1.5154	2	6	0.2933	
<i>constantinus</i> hw sex	1	0.27887	0.96678	2	5	0.4416	
<i>cresphontes</i> fw sex	1	0.42635	0.74322	2	2	0.5737	
<i>cresphontes</i> hw sex	1	0.75524	1.5428	2	1	0.4947	
<i>dardanus</i> fw sex	1	0.045761	2.0381	2	85	0.1366	
<i>dardanus</i> hw sex	1	0.53272	46.741	2	82	2.84E-14	**
<i>delalendei</i> fw sex	1	0.58043	2.7668	2	4	0.176	
<i>delalendei</i> hw sex	1	0.4957	1.4744	2	3	0.3581	
<i>troilus</i> fw sex	1	0.47228	3.1323	2	7	0.1068	
<i>troilus</i> hw sex	1	0.25238	1.1815	2	7	0.3613	

Table S2: MANOVA tests performed in this study. Symbols: * denotes $p < 0.05$ ** denotes $p < 0.01$ after Bonferroni correction.

Pairwise MANOVA: forewings

Color form	<i>cenea</i>	<i>hippocoon</i>	<i>niobe</i>	<i>planemoides</i>	<i>trophonius</i>	male-like
<i>cenea</i>		0.005775*	0.07275	0.03029	0.5111	0.004657*
<i>hippocoon</i>			0.9675	0.2962	0.01233	0.0139
<i>niobe</i>				0.3252	0.0294	0.06375
<i>planemoides</i>					0.04997	0.01791
<i>trophonius</i>						0.1766

Pairwise MANOVA: hind wings

Color form	<i>cenea</i>	<i>hippocoon</i>	<i>niobe</i>	<i>planemoides</i>	<i>trophonius</i>
<i>cenea</i>		0.001129**	0.03017	0.1279	0.1622
<i>hippocoon</i>			0.2703	0.6729	0.8499
<i>niobe</i>				0.7797	0.7433
<i>planemoides</i>					0.9414

Table S3: Pairwise MANOVA tests performed in this study. Symbols: * denotes $p < 0.05$ ** denotes $p < 0.01$ after Bonferroni correction.

VITA

The author was born in Pittsburgh, Pennsylvania. He obtained his Bachelor's degree in Ecology & Evolutionary Biology from Tulane University in 2014. He joined the University of New Orleans biology graduate program to pursue a Master's degree in biology, and became a member of the Penz/ DeVries lab in 2015.