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Locomotor Mimicry in Butterflies? The Associations of Positions of Centres of Mass among Groups of Mimetic, Unprofitable Prey

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Locomotor mimicry in butterflies? The associations of positions of centres of mass among groups of mimetic, unprofitable prey

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SUMMARY

With detailed measurements of flight-related morphological parameters of 18 species within the tribe Heliconiini and 10 of their non-heliconiine comimics, I found that morphological parameters relevant to flight biomechanics are associated with three escape tactics of these Neotropical butterflies: evasive flight, distastefulness, and mimicry. Two distinct character suites, one pertaining to the position of centre of body mass and another pertaining to wing shape, were identified using principal-components analysis. A third component correlated most highly with the position of centre of wing mass. Mimicry groups were best discriminated by the positions of centres of body and wing mass, suggesting that these features converged within mimicry groups. Centres of mass were positioned nearer to the wing base in mimicry groups composed of more palatable species, presumably decreasing the radial moments of inertia of the body and wings and increasing flight speed and turning performance. Predation has selected for body morphology that increases flight speed and manoeuvrability in palatable butterflies, whereas the morphology of distasteful species compromises flight performance. Convergent selection may reduce morphological differences of species within mimicry groups arising from distantly related lineages, and hence it may have enhanced the morphological diversification of palatable and unpalatable butterflies within lineages that have more recently evolved distastefulness.

1. INTRODUCTION

Natural selection favours attributes that improve predator avoidance, and a suite of morphological, behavioural and physiological characters is associated with the escape tactics of butterflies (table 1). In this paper, I focus on three escape tactics: the ability to fly fast and manoeuvre to evade predatory attacks (Chai 1990; Chai & Srygley 1990), the possession of defensive chemicals that are not only distasteful but may induce nausea or vomiting when ingested (see Brower (1984) and Bowers (1988) for reviews; also see Brown *et al.* (1991) for possible evolutionary scenarios), and colour, shape, and locomotor mimicry of 'unprofitable prey' (i.e. species that, because of their defences, are not worth pursuing (Baker & Parker 1979)).

Bates (1862) was the first to recognize the evolutionary significance of protective resemblance, and, in a sense, he was the first to recognize that two selective pathways, one via distastefulness and a second via mimicry, would reduce predation on adult butterflies. Mimicry may include the evolutionary convergence of flight pattern or body shape, in addition to coloration, even though the comimics derive from very different lineages and possess different palatabilities. Predation as the selective force on colour mimicry is well supported empirically (see Gilbert (1983) and Brower (1984) for reviews; also see Chai 1988; Mallet & Barton 1989) and theoretically (see Huheey (1988) for review). Using the classical definition, Batesian (1862) and Müllerian (1879) mimicry evolved with distasteful models, but Gibson (1974) demonstrated that mimicry of models which possessed efficient escape mechanisms also deterred predators. Therefore the evolution of mimicry is potentially an alternative selective pathway resulting in similarities among both palatable and unpalatable butterflies. In this paper, I will adopt Baker & Parker's (1979) terminology and refer to both distasteful models and palatable models that are difficult to catch as 'unprofitable prey'. Convergence of two unprofitable prey or convergence of a profitable prey on an unprofitable model are possible (e.g. Müllerian and Batesian mimicry, respectively; also see Van Someren & Jackson 1959; Thompson 1973). If the predator is capable of learning, its recognition and avoidance of mimetic unprofitable prey is enhanced by bright coloration (Gibson 1980).

I address two related questions that are relevant to insect flight. First, what morphological features improve evasive flight performance? Biomechanical analysis of forward flight in insects remains in its

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Table 1. *Butterfly morphology and life styles as prey*

ecology and physiology	palatable butterflies	unpalatable butterflies
predation	greater attack rate	greater survivorship[a]
defence	crypticity at rest	distasteful chemicals
flight pattern	fast, erratic or regular	slow and regular[a]
body shape	short and squat	long and thin[a]
allocation to thorax (flight muscle)	relatively large mass	relatively small mass[b,c]
allocation to abdomen (reproduction and digestion)	relatively small mass	relatively large mass[b,c]
centre of body mass (relative to the wing base)	just posterior	further posterior[d,e]
centre of wing mass	near to the wing base	positioned more distally[e]
manoeuvrability	more failed attacks	fewer failed attacks[a,d]
body temperature	relatively high	nearer to ambient[f]
microhabitat	open, sunlit	open or shaded[f]

[a] Chai & Srygley (1990).
[b] Srygley & Chai (1990*a*).
[c] Marden & Chai (1991).
[d] Srygley & Dudley (1993).
[e] This study.
[f] Srygley & Chai (1990*b*).

infancy. In an analysis of hovering flight among insect orders, Ellington (1984*a*,*b*,*c*) presented the most comprehensive evaluation of morphology, kinematics, and aerodynamics to date. Thus, as a first approximation, I will apply Ellington's methodology to the Lepidoptera as a crude biomechanical argument for factors affecting forward flight performance and manoeuvrability (Dudley 1990, 1991; Srygley & Dudley 1993).

Second, I am concerned with which morphological features serve as a reliable signal of unprofitability to the predators. We know that body shape (thoracic diameter: body length) is consistently longer and thinner in distasteful relative to palatable butterflies from the same lineage (Chai & Srygley 1990). This shape change is primarily due to the long, thin abdomens of distasteful butterflies, which position centre of body mass further posterior. A more posterior position of centre of body mass is associated with slower flight and more frequent captures by rufous-tailed jacamars when attacked (Srygley & Dudley 1993). However, lengthening the abdomen may also serve as a signal of distastefulness, due to the resulting long, thin flight profile (see examples in Chai & Srygley 1990). This signal may be made reliable by the corresponding reduction in flight performance. For example, in classic Batesian mimics, selection towards a body shape that signals distastefulness may be opposed by selection towards a shape that favours rapid acceleration when detected by predators.

This paper will focus on the tribe Heliconiini (Nymphalidae: Nymphalinae) and some of its non-heliconiine comimics (see figure 1). The useful features of Heliconiini are that: (i) it contains a diverse range of palatability states among its member species; and (ii) palatable and unpalatable species are associated within several coexisting mimicry groups that include members of other taxa. In this first paper in a series on the evolution of locomotor mimicry in the heliconiine butterflies and their mimics, I first identify correlated suites of Ellington's morphological features (1984*a*). Then I associate these features with mimetic resemblance to determine those that have evolved with colour signalling. Following adjustment for mimicry, and thereby assuming the traits are similarly independent of phylogeny, I associate these features with the palatability of butterflies to examine their evolution with forward flight performance and manoeuvrability (Srygley & Dudley 1993). I find that the positions of centres of body and wing mass are the best indicators of mimicry and palatability, whereas wing shape is not a reliable indicator.

2. STUDY SITES AND ORGANISMS

Adult butterflies were collected from two lowland, wet forest preserves in Panama: Barro Colorado Nature Monument (9°9′N,79°45′W, approximately 2700 mm annual rainfall; see Leigh *et al.* (1982) for further vegetation and climatic information), and Soberania National Park (approximately 2200 mm annual rainfall); and one lowland, wet forest preserve in Costa Rica: Sirena Station, Corcovado National Park (8°28′N,83°35′W; see Hartshorn (1983) for further information). In all localities, primary forest is interspersed with secondary growth of various stages.

Butterflies for all species from Corcovado and some from Panama were transported to Austin, Texas to establish greenhouse stocks. Butterflies were sampled from these stocks when possible. Otherwise, butterflies were captured in the field, placed in outdoor enclosures, and video-taped for analysis of flight kinematics and aerodynamics (R. B. Srygley, unpublished results). Captive butterflies were fed 10% honey-water in Panama, and 20–30% sugar-water supplemented with amino acids in Austin.

For exploratory multivariate analyses of the complete set of morphological features, sample sizes for heliconiine species and mimics ranged from 1 to 19 ($\bar{x}=6.4$), depending on abundance at the localities and ease of capture or rearing stocks (figure 1 legend). Species nomenclature follows Ackery & Smiles (1976) and DeVries (1987). Species were classified into one of six presumably monophyletic taxonomic lineages: Pieridae: Pierinae; Nymphalidae: Danainae/Ithomiinae complex, Charaxinae, and Nymphalinae: group I (including Heliconiini and Argynnini), group II

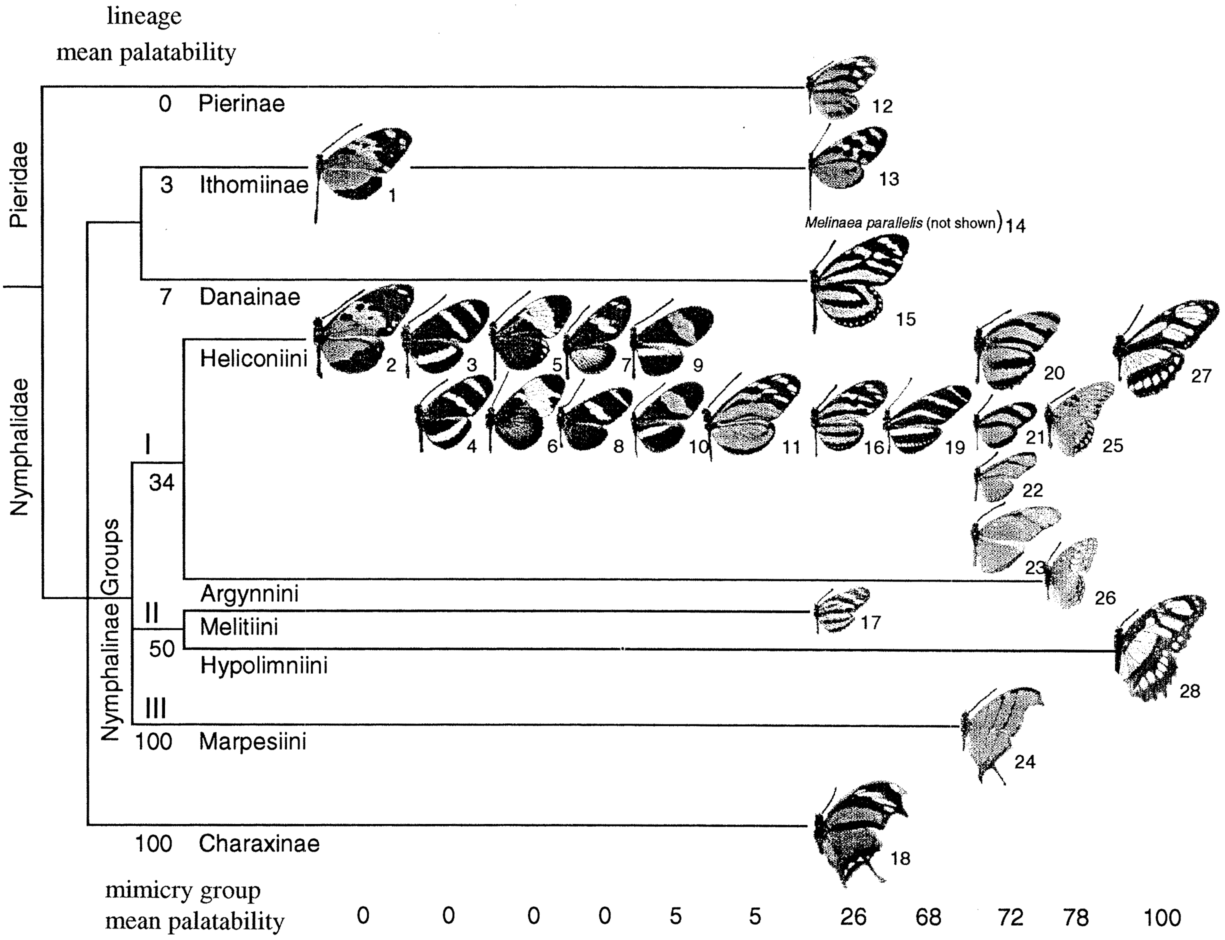

Figure 1. Classification of species into phylogenetic lineages and mimicry groups. Mean palatabilities (% eaten) of the phylogenetic lineages are scaled vertically from unpalatable (top) to palatable (bottom) on the tree branches. Mean palatabilities of mimicry groups are scaled horizontally from unpalatable (left) to palatable (right) below each group. Species (with sample sizes): 1, *Melinaea scylax* ($n=7$); 2, *Heliconius hecale melicerta* (11); 3, *H. pachinus* (10); 4, *H. hewitsoni* (10); 5, *H. cydno chioneus* (7); 6, *H. sapho candidus* (8); 7, *Laparus doris* 'blue form' (1); 8, *H. sara fulgidus* (12); 9, *H. melpomene rosina* (8); 10, *H. erato petiverana* (19); 11, *H. ismenius clarescens* (4); 12, *Perrhybris pyrrha* female (1); 13, *Mechanitis polymnia* (5); 14, *Melinaea parallelis* (1); 15, *Lycorea cleobaea* (2) 16, *Eueides isabella eva* (1); 17, *Eresia mechanitis* (2); 18, *Consul fabius* (2); 19, *H. charitonius* (9); 20, *Dryadula phaetusa* (12); 21, *Eueides lybia libioides* (5); 22, *E. aliphera gracilis* (3); 23, *Dryas iulia* (7); 24, *Marpesia petreus* (4); 25, *Agraulis vanillae incarnata* (8); 26, *Euptoieta hegesia* (1); 27, *Philaethria dido diatonica* (11); 28, *Siproeta stelenes* (7). Mimicry groups (from left to right): tiger 2, black/yellow, black/white, blue/yellow, black/red/yellow, tiger 3, tiger 1, zebra, orange, basal plan, green.

(including Melitiini and Hypolimniini), and group III (including Marpesiini). The higher classification and branching patterns follow Ackery (1984), and the divisions of Nymphalinae follow Müller (1888; see also Harvey 1991).

Before any statistical analysis, species were classified into one of 11 mimicry groups based on the colours and pattern on the upper side of the wings (figure 1). Four of these mimicry groups are composed of one pupal-mating *Heliconius* (numbers 4, 6, 8 and 10), and one *Heliconius* or *Laparus* that is not a pupal mater (numbers 3, 5, 7 and 9, paired respectively) (Gilbert 1991). Although molecular and morphological data are not in complete agreement, the pupal maters are believed to be grouped in a distinct clade relative to their sister species (Lee *et al.* 1992). The tiger mimics span the broadest phylogenetic range and include extremely distasteful Müllerian mimics, such as the ithomiines, and palatable Batesian mimics, such as the charaxine *Consul fabius*. I have divided the tiger mimics into three groups based principally on differences in their hindwings. The orange mimicry group is composed of *Dryas iulia* and *Marpesia petreus*, which appear very similar when flying (R. B. Srygley, unpublished observation), and *Eueides aliphera*, *E. lybia*, and *Dryadula phaetusa*, which are not as similar in flight as the others partly because of their size difference. Lastly, the basal mimicry group is composed of *Euptoieta hegesia*, *Agraulis vanillae*, and *Dione juno*, which have colour patterns similar to the nymphalid ground plan proposed by Nijhout (1991). Their coloration may be similar either because they share common ancestry or because the former two mimic the relatively distasteful *Dione juno*. The morphological data set was incomplete for *Dione juno*, and so it was not included in the exploratory analyses.

Palatability of a species was defined as the percentage of butterflies eaten of those presented to the rufous-tailed jacamar (*Galbula ruficauda*) (see Chai 1987, 1990; Chai & Srygley 1990 for details). Although the distribution of palatability is bimodal for butterfly species, I treat it as a continuous variable (Turner 1984) with a range of 0–100% eaten for this analysis. Blue-jays, silverbeak tanagers, Parson's tanagers (data from Brower 1984), and jacamars did not differ significantly in their preferences (percentage eaten) for eight genera of neotropical butterflies (Kruskall-Wallis H (corrected for ties) $= 3.05$, $0.5 > p > 0.3$). Therefore, palatability measures are generally applicable to other avian predators. Observations of birds (Chai 1986), beak marks on butterfly wings (L. Gilbert, unpublished results), and feeding trials (Chai 1987) are evidence that natural selection by predation is currently operating in lowland neotropical rainforests. Hence, I assume that palatability of lowland rainforest butterflies in Costa Rica is also a measure of past and current selection pressure on butterflies 425 km away in Panamanian lowland rainforest.

3. MORPHOLOGICAL MEASUREMENTS

Butterflies killed within 1 h in a cyanide jar were weighed on a Mettler AE-163 balance in Panama or a Cahn Electrobalance® RTL (both accurate to ± 0.1 mg) in Austin, and lengths were measured with Manostat calipers (accurate to ± 0.01 mm). Body mass, body length, thoracic diameter, and wing length were measured. Wings and legs were then removed, and lengths and masses of the head, thorax, and abdomen were measured. For the analyses that follow, masses and lengths of body segments were non-dimensionalized by dividing by body mass and length, respectively. Thoracic diameter was adjusted for body size (non-dimensionalized) by dividing by thoracic length, and wing length was non-dimensionalized by dividing by body length.

Note that the use of ratios may be problematic for statistical analyses because variation in the ratio may arise from changes in the numerator, the denominator, or both (see Packard & Boardman 1987). With the use of ratios and parametric statistics, I assume that either these morphological parameters scale isometrically with the size parameters with which they are non-dimensionalized or that deviations from isometry do not qualitatively affect the results. Furthermore, my application of Ellington's (1984*a*) techniques allows comparisons with his and other researchers' measures of flight-related morphology, kinematics, and aerodynamics in flying insects.

From a single wing pair positioned with the costal margin of the hindwing underlying the posterior margin of the forewing, wing area was measured with a digital leaf area meter (Delta-T Devices AMS, accurate to $\pm 0.01\ \text{cm}^2$, i.e. ± 0.3% of the smallest wing area measured), and used to calculate aspect ratio ($\text{Æ} = 4(\text{wing length})^2/2(\text{wing area})$). In the same position, the wing pair was then traced onto graph paper, and the radii of its outline from fore- to hindwing were measured at 5 mm spanwise intervals (see Dudley 1990; Betts & Wootton 1988 for details). The area was estimated for each wing segment, then the first, second, and third moments of the wing area, corresponding to the centroid, variance, and skewness of the distribution of area, were calculated (see Ellington (1984*a*) for formulae). Lastly, the overlapping wing pair was cut perpendicularly to the wing span at 5 mm intervals. Wing segments were weighed (± 0.01 mg), corrected for mass lost during cutting, and the first and second moments of wing mass calculated (for further discussion, see Ellington 1984*a*; Dudley 1990). The second wing pair was stored intact as a voucher for classification of the butterflies into mimicry groups.

In many butterfly species, the portion of the wing that is proximal to the wing base lies against the abdomen during flight. This portion may not be relevant to calculations of the moment of inertia of the wing, and thus I excluded it in a second calculation of the first and second moments of wing mass. To estimate the mean centres of mass as accurately as possible, I included all of the data that are currently available. Unfortunately, the raw data for some species were no longer available, and hence the number of species and each sample size differs from that presented in figure 1. These adjusted values for the centres of mass (see Appendix 1) were associated with mimicry and palatability in an *a posteriori* analysis.

Additional gross morphological parameters, including mean body diameter, mean wing thickness, mean wing chord, and virtual wing mass, were estimated. Virtual wing mass is the increase in the inertia of the wings due to the additional inertia of the air that must be accelerated during lift production. Body diameter was non-dimensionalized by dividing by body length. Mean wing thickness and wing chord were non-dimensionalized by dividing by wing length. Virtual wing mass was non-dimensionalized by dividing by the virtual mass of a hypothetical wing of equal length but constant width equal to the mean wing chord (see Ellington (1984*a*) for formulae and additional details).

To estimate the position of the centre of body mass from the mass and lengths for each of the body segments, I assumed that the centre of body mass was located on the body axis and each segment had equivalent density. The mass and lengths of four segments were used: the head, thorax, and the abdomen, which was cut at approximately one half of its length to make two segments. The wing base was assumed to be in the centre of the thoracic segment. I then iterated the net torque about each of 100 points spaced evenly along the body length. The point where the net torque was nearest to zero was the best estimate of the position of centre of body mass. Centre of body mass is expressed relative to the anterior end and the wing base. The radius of gyration for the net torque about the body axis was estimated and non-dimensionalized as a fraction of body length (see Dudley (1990) for details).

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4. STATISTICAL ANALYSES

(*a*) *Identification of character suites*

To condense the large number of morphological variables into fewer orthogonal components and identify covarying character suites, principal-components analysis was applied to the correlation matrix of 20 non-dimensional measures of morphology. The species' mean for each trait was entered into the analysis. Principal-components analysis maximizes the variation in the data set explained by as few components as possible (Kleinbaum *et al.* 1988).

To meet the assumptions of principal-components analysis, seven highly colinear variables were removed before the analyses. The first, second, and third moments of the non-dimensional wing shape and virtual wing mass, and the first and second moments of non-dimensional wing mass, were highly collinear (also see Ellington 1984*a*; Betts & Wootton 1988). For wing shape and virtual wing mass, only the first moment (equal to the mean) was entered to represent all three moments in the principal-components analysis. Similarly, for centre of wing mass, the mean was entered to represent the first two moments. Relative thoracic diameter and body diameter were also highly correlated, and hence the former was selected to represent both measures because it relates functionally to the contractile force of flight muscle. Relative abdominal length and thoracic length were inversely correlated, and both parameters pertain to flight. Because it directly affects the position of centre of body mass, relative abdominal length was entered into the analysis. The resulting data set had 13 non-dimensional morphological variables.

The morphological variables were correlated with the principal components (PCs), and those that were most heavily weighted (i.e. high correlations) were identified. This method identifies the character suites for which selection may be operating on one or more variables (see Cheverud 1982). I have named the PCs to summarize the character suites that they describe. To avoid confusion with the original morphological variables, non-dimensionalized positions of centres of body and wing mass relative to the wing base are abbreviated in lower case letters (e.g. cm$_{\mathrm{body}}$ and cm$_{\mathrm{wing}}$, respectively), and PCs are abbreviated in upper case letters (e.g. CM$_{\mathrm{BODY}}$ or CM$_{\mathrm{WING}}$).

(*b*) *Identification of characters associated with mimicry and palatability*

Species values for the PCs were entered into a stepwise discriminant function analysis (SAS version 6.0) to identify those that best discriminated among mimicry groups. Significant discriminants indicated that these or related characters were subject to convergent selection to improve mimicry. Mean PC values for mimicry groups were calculated to remove the average effect of mimicry in associating morphology with palatability.

To adjust for the effects of mimicry, mean PC values for each mimicry group were associated with the mean palatability of the mimicry groups. I used stepwise regression analysis (stepwise procedure; SAS version 6.0) to determine the principal components that correlated most highly with palatability among mimicry groups. Baker & Parker (1979) discussed the benefits and limitations of multiple regression analysis. Note that palatability is an individual trait for which Chai & Srygley (1990) estimate a species mean; this analysis ignores the variance within species and among birds. Here, I calculate the mimicry group palatability as the mean value for species within each mimicry group (for mean values, see figure 1).

Table 2. *Correlations of non-dimensionalized morphological variables with the first three principal components*

(Those variables correlating most highly are typed in bold-face.)

	PC1 (CM$_{\mathrm{BODY}}$)	PC2 (WING SHAPE)	PC3 (CM$_{\mathrm{WING}}$)
centre of body mass from wing base	**0.93**	0.29	−0.17
radius of gyration	**0.96**	0.22	−0.08
abdominal length	**0.87**	−0.18	0.40
abdominal mass	**0.80**	−0.18	−0.45
wing centroid	0.35	**0.83**	0.25
virtual wing mass	−0.12	**0.76**	0.43
wing thickness	−0.24	**0.61**	0.16
centre of wing mass	−0.29	0.09	**0.75**
body length/wing length	0.64	−0.11	**0.65**
relative thoracic mass	**−0.90**	−0.02	0.05
relative thoracic diameter	**−0.79**	0.21	−0.53
aspect ratio	0.40	**−0.68**	−0.22
centre of body mass from head	0.51	0.57	−0.56
variance explained (%)	42.8	22.9	16.6

3. RESULTS

(*a*) *Character suites*

The first five PCs were selected to represent the original data set because they explained 92.8% of the variance and the subsequent PCs explained greatly diminishing fractions. PC1–3 explained 82.3% of the variance in the data set (table 2). The first and second PC's defined distinct character suites: PC1 (CM$_{\mathrm{BODY}}$) was heavily weighted by body shape and mass allocation to the thorax and abdomen, and PC2 (WING SHAPE) was heavily weighted by wing shape, wing thickness, and virtual wing mass. This result shows that, following adjustment for body size, features pertaining to the body and wings vary to a large degree independently of one another.

The biological interpretation of the third PC is less clear than that for CM$_{\mathrm{BODY}}$ and WING SHAPE. PC3 (CM$_{\mathrm{WING}}$) was most heavily weighted by cm$_{\mathrm{wing}}$; however, the correlation of cm$_{\mathrm{wing}}$ with PC3 was weaker than those characterizing CM$_{\mathrm{BODY}}$ and WING SHAPE (see table 2). Moreover, other features which do not pertain to the wings alone were also highly correlated, e.g. body length relative to wing length. Hence, no character suite was realized in PC3, but the associations of CM$_{\mathrm{WING}}$

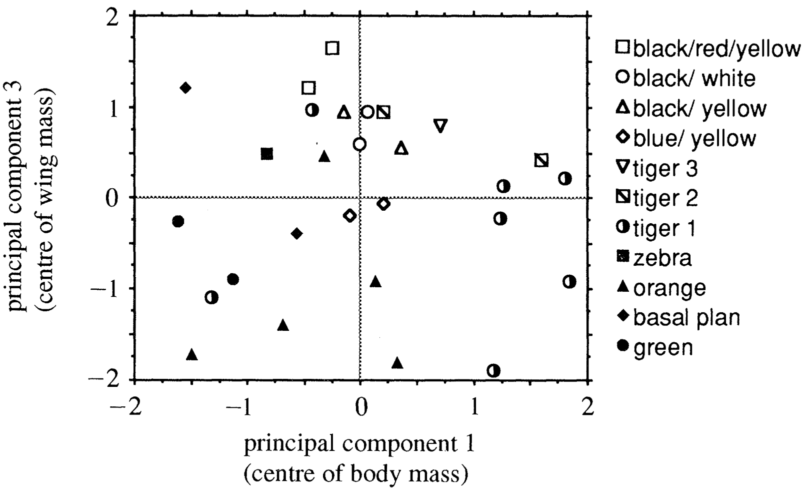

Figure 2. Principal component axes discriminating 11 mimicry groups. Mimicry groups are ordered from unpalatable (open symbols), to intermediate (hatched symbols), to palatable (filled symbols).

with mimicry and palatability are suggestive of its biological importance (see below).

PC4 and PC5 only explained an additional 10% of the variance, but they were included in the discriminant function and regression analyses. PC4 was most heavily weighted with wing thickness, and PC5 with cm$_{\text{wing}}$. Relative to the first three components, these latter two have minor roles in the discriminant function and regression analyses, and will be ignored in further discussion.

(*b*) *Morphological features associated with mimicry*

Among mimicry groups, CM$_{\text{WING}}$ was the first discriminant selected (figure 2; $\lambda = 0.401$, $p = 0.044$). Addition of CM$_{\text{BODY}}$ greatly improved the model ($\lambda = 0.185$, $p = 0.028$) such that 82% of the variance was accounted for. No other variables were selected. The discriminant function analysis indicates that both CM$_{\text{WING}}$ and CM$_{\text{BODY}}$ have greater variance among mimicry groups relative to within-mimicry group variance. However, only one or a few species occur within some of the mimicry groups. As a result, differences in sample sizes and correlation matrices exist among the groups, violating an assumption of discriminant function analysis. None the less, convergent selection due to mimicry may be operating on variables within CM$_{\text{WING}}$ or CM$_{\text{BODY}}$, constraining the independent evolution of those variables within mimicry groups. For example, if mimicry between two palatable, fast-flying species evolves first, a transition to unpalatable in one species may not result in its transition to slow flight because counterselection maintains its protective coloration and flight behaviour.

Table 3. *Stepwise regression analysis of the dependent variable mean palatability and five independent principal components*

($\alpha = 0.15$ to enter or remove. Resultant equation: palatability $= 34 - 30(\text{CM}_{\text{BODY}}) - 24(\text{CM}_{\text{WING}})$.)

variable entered	SS	d.f.	MS	F	p	model R^2
PC1: CM$_{\text{BODY}}$	3953	1	3953	19.51	0.0031	0.653
PC3: CM$_{\text{WING}}$	2890	1	2890	14.26	0.0069	0.824
error	2679	8	335	—	—	—

(*c*) *Morphological features associated with palatability*

Among mimicry groups, CM$_{\text{BODY}}$ was selected as the first determinant of mimicry group palatability (table 3). The association is negative, suggesting that abdominal lengths are shorter and cm$_{\text{body}}$ is proximal to the wing base in mimicry groups composed of more palatable species relative to those composed of unpalatable ones. In addition, thoracic diameter and mass increases and abdominal mass decreases with increasing palatability. CM$_{\text{WING}}$ was the second component selected. Its negative correlation with mimicry group palatability suggests that cm$_{\text{wing}}$ is proximal to the wing base in palatable mimicry groups relative to its position in unpalatable ones.

The associations among palatability and the centres of body and wing mass were confirmed in a stepwise regression analysis of the positions of centres of mass available for 28 species (centre of wing mass adjusted for area behind the wing base; see Morphological Measurements and Appendix 1). With respect to order of entry, cm$_{\text{body}}$ and cm$_{\text{wing}}$ were selected as significant predictors of palatability ($r = 0.689$, $F = 11.27$, $p < 0.001$), and the positions of centres of mass lie nearer to the wing base in more palatable species.

4. DISCUSSION

(*a*) *Relevance of centre of body mass to escape tactics*

This research is the first detailed, functional analysis of flight morphology in relation to the response to natural selection by predation. Principal components associated with the positions of centres of body and wing mass best discriminated the mimicry groups.

Groups composed of palatable species diverged from those composed of distasteful ones in these same components. Resolution of the heliconiine phylogeny will allow confirmation of the hypothesized convergence in the positions of centres of body and wing mass within mimicry groups.

The first principal component is directly relevant to flight speed because allocation of more mass to the thorax and less to the abdomen is indicative of faster flight in butterflies (Srygley & Chai 1990*a*). Additional flight muscle mass in the thorax increases the power available for flight (Ellington 1991). Furthermore, the first principal component is also directly relevant to flight manoeuvrability. Positioning $\mathrm{cm}_{\mathrm{body}}$ near to the wing base reduces the body's radial moment of inertia, and thus its position is important for maximizing angular acceleration and manoeuvrability (Ellington 1984*a*,*b*). In a comparison of 28 butterfly genera, Srygley & Dudley (1993) identified $\mathrm{cm}_{\mathrm{body}}$ as the best predictor of butterfly flight speed, palatability, and successful evasion of jacamar attacks in a small cage.

The flight pattern of distasteful butterflies is more regular than that for palatable species (for examples of flight profiles and patterns, see Chai & Srygley (1990)). Positioning $\mathrm{cm}_{\mathrm{body}}$ more distally on the abdomen may smooth the flight pattern because the inertia of the abdomen, which in butterflies composes the majority of the body mass (Srygley & Chai 1990), counterbalances the torques that are generated by the wing and act directly on the thorax. For any given torque, angular acceleration about the wing base is less than that for palatable butterflies. Moreover, the narrow junction between thorax and abdomen may allow the weight of the abdomen to bob with little effect on the thorax. Oscillations of the abdomen might dampen forces generated by the wings while minimizing oscillations of the thorax and associated effects on stroke angle.

Although manoeuvrability of unpalatable butterflies is reduced, the regular flight pattern invokes considerable savings in energetic costs. Generation of an erratic flight pattern can incur a cost as great as 55% (43% on average) of total specific power requirements for flight (Dudley 1991). In contrast, the power required to rotate the body axis about its centre of body mass was less than 1% of the power required to generate an erratic flight pattern. The magnitude of this difference between palatable and unpalatable butterflies is being investigated.

Convergence in $\mathrm{cm}_{\mathrm{body}}$ among species within mimicry groups might result in convergence in oscillations of the body during flight. By affecting the position of $\mathrm{cm}_{\mathrm{body}}$, the long and slender abdomens of unpalatable butterflies may function to signal more clearly their distastefulness to predators at the expense of any ecological benefits gained from greater flight speed or manoeuvrability. Furthermore, their long and slender abdomens protrude behind and frequently hang below the hindwings during flight (for examples, see figure 1 in Chai & Srygley (1990)). Possession of a flight profile or generation of a flight pattern that is distinct from those of palatable species enhances communication and benefits both the distasteful prey and predators. Moreover, without distastefulness, generation of a regular flight pattern and reduction in manoeuvrability would be strongly selected against, and thus difficult for palatable 'cheaters' to mimic.

Finally, the long, slender body morphology of unpalatable species may serve to reduce damage during capture and handling. Slow, regular flight patterns are easier to predict and intercept. Longer bodies are more easily grasped. Of those captured which were released or escaped, survivorship among unpalatable butterflies was higher than among palatable ones (Chai 1990). When handled, unpalatable butterflies bend their long abdomens in a 'C' shape towards the predator and often evert pungent scent glands as a reinforcement.

(*b*) *Relevance of centre of wing mass to escape tactics*

The position of $\mathrm{cm}_{\mathrm{wing}}$ directly affects the radial acceleration and inertia of the wings during acceleration and deceleration during the wing stroke (Ellington 1984*b*,*c*). As a result, convergence of $\mathrm{cm}_{\mathrm{wing}}$ among species within mimicry groups may be associated with convergence in acceleration of the wing stroke and wingbeat frequency. Perhaps, as is hypothesized in bat–moth interactions, wingbeat frequency is detected and learned by avian predators such that convergence in $\mathrm{cm}_{\mathrm{wing}}$ improves the prey's warning signal to potential predators.

Relative to members of unpalatable mimicry groups, those in more palatable groups position $\mathrm{cm}_{\mathrm{wing}}$ near to the wing base reducing the inertia of the flapping wings and favouring rapid wing acceleration during the wing stroke. Flight speed probably increases with wingbeat frequency (Betts & Wootton 1988) such that positioning $\mathrm{cm}_{\mathrm{wing}}$ near to the wing base may be especially important to palatable butterflies during acceleration to elude predators. Furthermore, positioning $\mathrm{cm}_{\mathrm{wing}}$ near to the wing base has an energetic advantage. For 15 Neotropical butterfly species, estimates of costs to overcome the inertia of the wings, including that due to the virtual wing mass, typically exceeded aerodynamic power requirements by a factor of three (Dudley 1991).

Wing shape, wing venation, or wing thickness may affect the position of $\mathrm{cm}_{\mathrm{wing}}$. Those wings which are broad near the base but taper distally position $\mathrm{cm}_{\mathrm{wing}}$ nearer to the base than even or expanding wing shapes. Reducing the density of venation or wing thickness in distal parts of the wing also results in a more proximal $\mathrm{cm}_{\mathrm{wing}}$. For example, unpalatable butterflies might have more wing venation or greater wing thickness near the wing tips to assure durability when grasped. In contrast, palatable species might have fewer structural components near the wing tip to permit breakage allowing escape from the predator's grasp.

(*c*) *Relevance of wing shape to flight*

For the heliconiines and the non-heliconiine mimics, the evolution of wing morphology is appa-

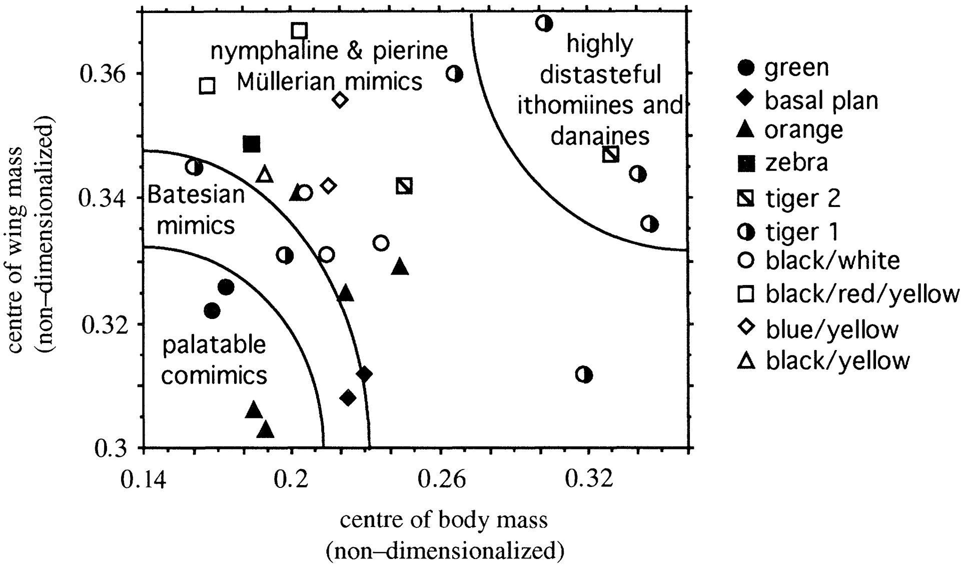

Figure 3. Centre of wing mass against centre of body mass for the 27 butterfly species listed in Appendix 1. Hypothetical adaptive zones are depicted with curvilinear lines, which are not meant to represent contours of selection gradients. In the lower left corner, the most palatable species are found near their respective comimics where centres of mass are positioned near to the wing base. In the upper right, highly distasteful ithomiine and danaine models are found where centres of mass are positioned furthest from the wing base. Nymphaline and pierine Müllerian mimics lie between these two adaptive zones, and those that are comimics of the ithomiines and danaines lie nearer to that zone than do other species. Batesian mimics lie just outside of the zone of palatable species. See text for hypothesized evolutionary scenarios.

rently independent of changes in body morphology. Strauss (1990) also found that wing and body morphology of heliconiines and ithomiines are generally uncoupled in size and shape, and thus he concluded that the wing and body evolve as separate character suites. In contrast to body-shape parameters, wing shape parameters, which are important components of aerodynamic theory of flight, do not play a significant role in discriminating mimicry groups or predicting palatability. Dudley (1990) found no correlation of aspect ratio with forward flight speed, a result consistent with the present study.

Two hypotheses are proposed for the lack of wing-shape convergence. First, conflicting selective forces may be operating on components of WING SHAPE, because first, second, and third moments of wing area are highly correlated (Ellington 1984*b*; Betts & Wootton 1988). During hovering, the second moment of wing area is theoretically proportional to the mean lift force generated by the wings (Ellington 1984*b*,*c*). However, the third moment of wing area is proportional to the mean profile power on the wings due to friction drag and separation of air flow from the upper wing surface (for further discussion see Ellington 1984*b*,*c*; Pennycuick 1989). Relative to a position closer to the wing base, a distal positioning of wing centroid (first moment of wing area) is associated with greater force production with each wing stroke (second moment) and also greater induced drag on the wings (third moment).

Second, the evolution of contrasting border colours that outline the wing (e.g. in the tiger mimicry group) may make precise wing shape convergence unnecessary (L. Gilbert, personal communication). For example, *Consul fabius* has an angular forewing apex that is similar in shape to many other charaxines (figure 1). However, the contrasting pattern of yellow on the dark apical margin may create a false, curvilinear edge to the margin during flight activity such that the apex appears more similar to the rounded apices of the highly distasteful models. Wing shapes may not be more similar for another reason: only a slight resemblance to noxious prey may be sufficient to deter some predators from attack (for an example, see Dittrich *et al.* 1993).

(*d*) *Locomotor mimicry in an adaptive landscape*

At opposite ends of the palatability spectrum, palatable and highly distasteful butterflies lie near two peaks in an adaptive landscape (figure 3). Relative to unpalatable species, palatable butterflies cluster near to where body shape and mass distribution biomechanically maximize flight speed and manoeuvrability. In one corner of figure 3, palatable members of Nymphalinae groups I, II, and III position the centres of body and wing mass near to the wing base. Furthermore, within this zone, comimics, such as *Philaethria* and *Siproeta* or *Dryas* and *Marpesia*, are very similar to one another.

At the other extreme, the danaines and ithomiines, which are presumably models of Müllerian mimicry complexes, position $\mathrm{cm}_{\mathrm{body}}$ and $\mathrm{cm}_{\mathrm{wing}}$ further from the wing base than any other species. These unpalatable butterflies cluster where body and wing morphology compromise flight speed and manoeuvrability, presumably to improve their conspicuousness, avoid

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being confused for palatable butterflies (Fisher 1958; Brower *et al.* 1971; Turner 1984; Guilford 1986; Chai 1990; Srygley & Dudley 1993), and reduce energetic costs of flight (Dudley 1991).

Müllerian mimicry may accelerate the morphological diversification among palatable and unpalatable species within a lineage. Within Nymphalinae groups I and II, transitions to distastefulness and associated divergences in the positions of centres of mass may have evolved more recently than distastefulness in the danaines and ithomiines (Srygley 1991). The positions of the centres of mass for distasteful species within Nymphalinae groups I and II generally lie between the two extremes set by the palatable members of the Nymphalinae and the highly distasteful Ithomiinae and Danainae (see figure 3: Müllerian mimics). As a result of transitions in palatability within the lineages, body morphology diverged, but tiger mimics of the older danaine and ithomiine models may have had additional convergent selection operating due to mimicry. This hypothesis of accelerated evolution is testable with comparisons of body morphology from heliconiine species which mimic the older ithomiines to that of sister species which do not.

As a qualitative example, *Heliconius hecale* and *Eresia mechanitis*, distasteful tiger mimics from groups I and II, lie nearer to the zone of the danaine and ithomiine models than any of the other species. As long as the palatabilities of the sister species are equal, I would predict that mimics would have positioned centres of mass nearer to that of the ithomiine models than closely related non-mimics. Currently, neither the resolution in the heliconiine and melitiine phylogenies nor the data for $\mathrm{cm}_{\mathrm{body}}$ and $\mathrm{cm}_{\mathrm{wing}}$ are available for an adequate test. However, the association of centres of mass with the mean palatability of mimicry groups is evidence that mimicry and palatability generally operate in concert.

Characters for evasive flight in palatable species are incongruent with the morphology of distasteful ones, which ultimately makes a 'good' Batesian mimic with the morphology and flight pattern of unpalatable butterflies very difficult to evolve. In the zone of Batesian mimicry (figure 3), *Consul fabius* positions $\mathrm{cm}_{\mathrm{body}}$ near to the wing base like other palatable species, whereas it positions $\mathrm{cm}_{\mathrm{wing}}$ further from the wing base and near to that of its distasteful ithomiine and danaine models. Associated with its body morphology, *C. fabius* is capable of flying rapidly relative to its models to evade predators when its coloration is insufficient for masquerade (R. B. Srygley, unpublished observations; see also discussion of mimicry in Srygley & Chai (1990*a*)).

Because Batesian mimics are not released following capture, selection may favour predator avoidance once detected. Therefore, Batesian mimics may retain features that contribute to flight speed and manoeuvrability. In contrast to this study, Huheey (1988), echoing Fisher (1930), Cott (1940) and Sheppard (1958), argued that Batesian mimics will evolve to appear more similar to the model than Müllerian mimics; Turner (1984) argued that, although the model may evolve away from the Batesian mimic (i.e. advergence (Brower & Brower 1972)), the mimic evolves more rapidly to appear like the model.

As a result of selection on body shapes that favour manoeuvrability to escape predators when detected, the evolution of Batesian mimics to appear like their model may be sufficiently slowed to determine which features change first to improve locomotor mimicry and which features change last to retain the ability to escape. The morphology of *Consul fabius* suggests one possible scenario. Following the evolution of mimetic resemblance of the tiger models, selection to position the centres of mass further from the wing base would be opposed by counterselection for evasive flight when detected by predators. Perhaps the position of centre of wing mass changes first (due, in part, to changes in wing shape) to change the associated wing kinematics and improve deception during flight. Reallocation of thoracic mass to the abdomen and lengthening of the abdomen might follow, repositioning the centre of body mass posteriorly and resulting in a loss of manoeuvrability. Batesian mimicry should be a fertile field for future investigation of the evolution of flight-related morphology and kinematics.

Examining heliconiines and ithomiines, Strauss (1990) also found a high degree of within-lineage variation in body morphology, especially in the heliconiines, but he did not associate it with palatability or mimicry. From the present study, I attribute the variation in heliconiine body morphology to predation via two selective pathways: (i) divergent evolution due to palatability changes within the heliconiines; and (ii) convergent evolution due to mimicry of non-heliconiines.

In the future, improvements in the phylogenies, biomechanics, and biometrics that I have applied in this exploration will all refine investigations of locomotor mimicry. First, more resolved phylogenies are needed to elucidate convergence from similarity due to phylogenetic relatedness, especially among the heliconiines. We need confirmation that members of the *Heliconius* mimicry groups included in this study arise from distinct lineages (Brown 1981; Lee *et al.* 1992). As better phylogenies become available, more rigorous statistical analyses can be applied to the phenomenon of convergent evolution. Second, measures of body and wing kinematics are needed to confirm the hypothesized functional explanations for the body and wing morphology. Similarities in the oscillating frequency of the body and wings are predicted to arise within mimicry groups, in part, because rotation of the body and wings is dependent on the positions of the centres of mass. Third, more precise measures of wing shape are needed to confirm that wing shape and mimicry are not associated. With respect to mimicry, future investigations into wing shape should include morphometrics with greater resolution than those applied to current analysis of insect flight biomechanics.

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APPENDIX 1

taxonomic group: species	*n*	relative cm_{body} (mean ± s.d.)	*n*	relative cm_{wing} (mean ± s.d.)	*n*	palatability (% eaten)[a]
Pieridae: Pierinae:						
Perrhybris pyrrha female	2	0.207 ± 0.007	2	0.312 ± 0.015	8	0
Nymphalidae: Ithomiinae:						
Melinaea scylax	6	0.329 ± 0.009	8	0.347 ± 0.007	29	5
M. parallelis	2	0.302 ± 0.055	2	0.368 ± 0.004	—	5[b]
Mechanitis polymnia	8	0.340 ± 0.012	5	0.344 ± 0.003	26	0
Danainae:						
Lycorea cleobaea	2	0.345 ± 0.039	2	0.336 ± 0.001	28	7
Nymphalinae group I:						
Agraulis vanillae	12	0.223 ± 0.010	5	0.308 ± 0.005	12	75
Dione juno	12	0.229 ± 0.010	3	0.312 ± 0.013	12	20
Dryadula phaetusa	26	0.222 ± 0.008	21	0.325 ± 0.002	16	88
Dryas iulia	23	0.184 ± 0.009	16	0.306 ± 0.005	24	92
Philaethria dido	16	0.173 ± 0.011	15	0.326 ± 0.003	12	100
Eueides lybia	4	0.202 ± 0.015	3	0.341 ± 0.017	33	39
E. aliphera	6	0.244 ± 0.013	6	0.329 ± 0.015	36	39
E. isabella	1	0.197	1	0.331	8	50
Laparus doris	6	0.215 ± 0.018	2	0.342 ± 0.006	35	0
Heliconius hecale	13	0.246 ± 0.012	14	0.342 ± 0.006	30	0
H. melpomene	22	0.203 ± 0.008	10	0.367 ± 0.007	20	10
H. cydno	13	0.214 ± 0.014	8	0.331 ± 0.009	2	0
H. pachinus	20	0.189 ± 0.009	10	0.344 ± 0.005	22	0
H. eleuchia	1	0.236	1	0.333	—	0[b]
H. sara	19	0.220 ± 0.009	18	0.356 ± 0.005	6	0
H. erato	10	0.166 ± 0.007	20	0.358 ± 0.004	32	0
H. sapho	13	0.205 ± 0.011	8	0.341 ± 0.004	—	0[b]
H. charitonius	22	0.183 ± 0.007	1	0.349	24	62
Nymphalinae group II:						
Eresia mechanitis	3	0.266 ± 0.030	2	0.360 ± 0.001	—	0[b]
Siproeta stelenes	13	0.167 ± 0.016	11	0.322 ± 0.004	18	100
Nymphalinae group III:						
Marpesia petreus	13	0.189 ± 0.008	13	0.303 ± 0.005	1	100
Charaxinae:						
Consul fabius	4	0.160 ± 0.014	3	0.345 ± 0.013	10	100

[a] Palatability data from Chai (1990).

[b] Palatibility assumed to be equal to that of closely related species.

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