CORRELATIONS OF THE POSITION OF CENTER OF BODY MASS WITH BUTTERFLY ESCAPE TACTICS

By ROBERT B. SRYGLEY* AND ROBERT DUDLEY

Department of Zoology, University of Texas, Austin, Texas 78712, USA and *Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama*

Summary

Using the evolution of neotropical butterflies as a natural experiment, we examine Ellington's biomechanical hypothesis that the position of center of body mass affects insect maneuverability. We find that the position of center of body mass is correlated with the butterflies' palatability, natural flight speeds and their ability to evade predators in a small cage. Relative to distasteful species, palatable butterflies fly faster and maneuver more successfully to evade attacks from aerial predators. The large thorax and short abdomen of palatable species position the center of body mass near to the wing base, whereas the mass allocation and body shape of distasteful butterflies position center of body mass further posteriorly. The position of center of body mass is an important indicator of flight performance, including both aerial maneuverability and flight speed, that warrants incorporation into future studies of invertebrate and vertebrate flight.

Introduction

Ellington (1984*a*,*b*) suggested that insects may position the center of body mass near to the wing base in order to enhance maneuverability. Positioning the center of body mass near to the wing base increases the responsiveness of the body to pitching moments generated by the wings and facilitates rapid changes in speed and direction of flight (Ellington, 1984*b*). For a rotating body, angular acceleration is inversely proportional to the body's moment of inertia, while the moment of inertia is proportional to the radius of gyration squared. The ease of measurement (Kreighbaum and Barthels, 1981; Alexander, 1982) and high correlation of the position of center of body mass with the radius of gyration (for butterflies, R. B. Srygley, unpublished data) thus make the position of center of body mass a useful predictor of the body's moment of inertia. However, since Ellington first proposed this hypothesis, it has not been examined further (but see Srygley, 1991).

Because flight performance is essential for predator foraging success and prey survival in aerial encounters, strong selection is likely to occur on flight-related morphology of aerial predators and their prey. For this reason, aerial predators or their prey are frequent

*Present address: Department of Ecology and Evolution, 1101 East 57th Street, University of Chicago, Chicago, IL 60637, USA.

subjects for analysis of flight-related morphology (e.g. Kenward, 1978; Norberg, 1986; Norberg and Rayner, 1987; Marden, 1989). Flight speed and maneuverability are two components of flight performance that are likely to be important in predator–prey interactions.

Neotropical butterflies (Hesperioidea and Papilionoidea) differ in palatability as assayed by an avian insectivore, the rufous-tailed jacamar (*Galbula ruficauda*; Chai, 1990). Central to the palatability syndrome in neotropical butterflies (Chai and Srygley, 1990; Srygley and Chai, 1990*a,b*; Srygley, 1991, and references therein) is an evolutionary change in flight speed and maneuverability. As a result, butterflies are an excellent group to associate flight speed and maneuverability with morphological parameters that biomechanical models have identified as relevant to flight. Previously among 53 neotropical species, Chai and Srygley (1990) found that body shape (thoracic diameter/body length) was a significant predictor of palatability, flight speed and the proportion of unsuccessful attacks by the rufous-tailed jacamar.

Here, we associate differences in butterfly escape tactics with flight-related morphology. We present measures of natural flight speeds for butterflies and test which of the flight-related morphological parameters are the best predictors of flight speed. We also test which of the flight-related morphological parameters are the best predictors of the ability to evade attack. The position of center of body mass proves to be indicative of palatability, flight speed and maneuverability.

Materials and methods

Measures of palatability and maneuverability

Palatability of a butterfly species was assessed as the percentage of individuals eaten of those presented to the rufous-tailed jacamar, a specialized avian insectivore, in Corcovado National Park, Costa Rica. For this analysis, we treat palatability as a continuous variable with a range of 0–100% eaten (for further details, see Chai and Srygley, 1990; Chai, 1990).

Chai presented 14–20 individual butterflies of distinct color morphs to the jacamar during each trial. In order to necessitate discrimination of palatable and distasteful morphs and prevent satiation, Chai simultaneously released distasteful to palatable species into the presentation cage in approximately a 2:1 ratio. He noted that distasteful butterflies frequently circled inside the cage in slow, regular flight patterns, whereas palatable morphs were disturbed by the birds' activities, resulting in fast, erratic flight patterns (see Chai, 1990, for further details). Because jacamars only respond to prey in motion, attacks were frequently initiated by the erratic responses of the butterflies. It is likely that the small size of the cage (0.94m in diameter by 0.92m in height; see diagram in Chai, 1990) prevented butterflies from reaching top flight speed, and thus they avoided the birds' attacks with linear and radial acceleration. As a result, the proportion of failed attacks is assumed to be an assay of maneuverability.

For the six species of butterflies measured in Panama, we assume that palatability and failed attacks are identical to those of closely related species or genera in Costa Rica. *Itaballia demophoon* and *Perrhybris pyrrha* are sister genera (0% eaten, 0% failed

attacks). *Eurytides ilus* (presumed to be a Batesian mimic of the highly distasteful *Parides lycimenes*) and *E. protesilaus* are sister species to *E. orabalis* (100% eaten, 0% failed attacks). *Olyras insignis* and *Godyris zygia* (0% eaten, 17% failed attacks) are comimics and members of the highly distasteful Danainae/Ithomiinae group. *Cissia* sp. is a sister species to *C. libye* (100% eaten, 40% failed attacks) and *Melinaea parallelis* is a sister species to *M. scylax* (3% eaten, 14% failed attacks).

Natural flight speeds

During September–October 1989 and May–July 1990, butterfly airspeeds were measured in the mornings (08:00h to noon) when light to moderate winds blew (0.2–3.8 m s^{-1}). We intercepted butterflies crossing Lake Gatún, an artificial lake flooded to form a large portion of the Panama Canal, or released cage-reared or field-captured individuals. We followed each butterfly in a 15 foot Boston Whaler powered with a 30 horsepower outboard motor until an even pace was maintained approximately 1 m aft or parallel to the starboard side for 10 s. Sampled butterflies remained within 1–2 m of the water's surface. A reliable estimate of airspeed was obtained by measuring the speed of the boat with a hand-held unidirectional anemometer (TSI model 1650). The anemometer probe was held laterally from the prow of the boat such that the probe tip was 1–1.5 m distant from the boat and at the same height as the flying butterfly. Both the butterfly and anemometer were kept out of the flow field around the boat's hull. Airspeed was thus measured directly and no assumptions concerning ambient wind were necessary (ground speed is equal to the vector sum of airspeed and wind). Between the lake center and edge, a maximum of three measurements of flight speed were taken before capture (also see DeVries and Dudley, 1990; Dudley and DeVries, 1990).

Measures of morphology

Following measurements of flight speed, butterflies were returned to the laboratory for analysis of flight-related morphology. Butterflies were killed in a freezer within 3 h of measuring flight speed. Masses were measured on a Mettler AE-163 balance (accurate to ±0.1 mg) 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. In order to estimate the position of center of body mass, the abdomen was cut at approximately one-half of its length, and the lengths and masses of the fore- and hind-halves of the abdomen were measured.

From a single wing pair positioned with overlapping costal margins (as near as possible to their position during flight), wing area was measured with a digital leaf area meter (Delta-T Devices AMS, accurate to ±0.01 cm^2). 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 span-wise intervals (see Betts and Wootton, 1988; Dudley, 1990, 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 (±0.01mg), 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). Moments of wing mass and wing area are relevant to quasi-steady aerodynamic analysis. The second moment of wing mass is proportional to the moment of inertia of the wing. At low advance ratios (forward velocity:flapping velocity), the second and third moments of wing area are proportional to mean lift and drag on the wing, respectively (for discussion of theory and methods, see Ellington, 1984*a–c*). The advance ratios for butterflies in natural flight have not been measured. However for the advance ratios characteristic of butterflies flying in an insectary (near 1; Dudley, 1991), the moments of wing area are not likely to be directly proportional to lift and drag, but they remain the dominant morphological determinants of these forces (C. Ellington, personal communication).

To estimate the position of the center of body mass from the mass and lengths for each of the body segments, we assumed that the center of body mass was located on the body axis and that each segment had equivalent density. We 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 center of body mass. The position of center of body mass was non-dimensionalized as a fraction of body length and expressed relative to the wing base (see Dudley, 1990, for additional details).

Statistical analyses

Airspeeds for butterflies that were released from the boat were pooled with those airspeeds for butterflies that were intercepted naturally crossing the lake because mean airspeeds for the two groups did not differ significantly.

Organisms that are alike solely as a result of their common ancestors violate the assumption of independent observations for parametric analyses, and thus inflate the degrees of freedom and chance of rejecting the null hypothesis when it is true. If the phylogeny is resolved, statistical tests are currently available to correct for problems of historical relatedness (Harvey and Pagel, 1991). However, the phylogeny of butterflies is not well resolved (Srygley, 1991). In order to alleviate problems of similarity by common descent, a nested analysis of variance (ANOVA) was performed (Harvey and Mace, 1982) on the dependent variable flight speed with four nested taxonomic levels as the independent variable: family, subfamily, genus and species. In order for variation in palatability to be retained at the generic level, one species (*Phoebis argante*) that differed from congenerics in palatability and one (*Eurytides ilus*) that differed from congenerics in that it is presumably a Batesian mimic were classified as unique genera in the ANOVA and regression analyses that follow (increasing $N=26$ to $N=28$ genera). Because the generic level was the only taxonomic level that explained a significant proportion of the variance in airspeed, the mean airspeed for each genus was used as a single, independent observation in further analyses.

Twelve features, five measured directly and seven derived, were entered into stepwise regression analyses of palatability, maneuverability and maximum airspeed. Those measured directly were: body mass, abdominal length, thoracic mass, thoracic diameter and wing area; those derived were: total virtual wing mass (i.e. the inertia of the wings
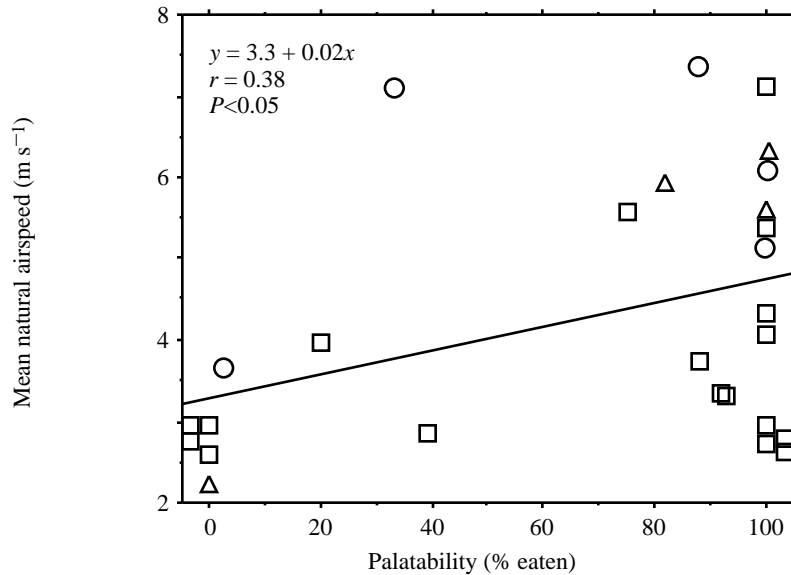
Fig. 1. The association between mean natural airspeed and palatability for 27 genera of neotropical butterflies. Although wing loading was a significant predictor of airspeed (see Table 4), adjustment of airspeed for wing loading (using the residuals of airspeed regressed on wing loading) improved the association with palatability by only 1% additional variance explained. A positive association is observed among genera within all three butterfly families represented: squares, Nymphalidae; triangles, Pieridae; circles, Papilionidae. Data points were shifted slightly to avoid overlap.

during flapping flight that results from acceleration of the air during lift production), wing loading and the following non-dimensionalized parameters: wing centroid (center of wing area/wing span), first moment of virtual wing mass, relative virtual wing mass, center of wing mass and center of body mass.

Results

Butterflies flew in nature at airspeeds (see Table 1) that were two to six times faster than groundspeeds obtained from the same genera in insectaries (Dudley, 1990; P. Chai, unpublished data). For the same set of butterflies, palatability was a significant predictor of mean natural airspeed (Fig. 1).

Of twelve flight-related morphological traits, the position of center of body mass (this positioning relative to the wing base is here abbreviated: cm_{body}) was the strongest single predictor of palatability for 27 neotropical butterfly genera (Table 2). Subsequently, in the forward stepwise regression, abdominal length, which was a determinant of cm_{body} (Table 3) and thoracic diameter, which is proportional to the cross-sectional area of the flight muscle and thus an indicator of its contractile force (Schmidt-Nielsen, 1989), together improved prediction of palatability by 20%.

The position of center of body mass was a significant predictor of both the butterflies' ability to escape from the jacamars and their natural flight speeds over the lake.

Table 1. *Taxonomy, palatability, maximum velocity (V) and variance (s²), and gross and derived morphological features for 36 butterfly species*

Family Subfamily	Genus	Species	Palatability (% eaten)	N	V (m s^{-1})	s^2	m (mg)	L (mm)	m_t (mg)	d_t (mm)	L_a (mm)	$\hat{l}_1$‡	R (mm)	S (cm²)	$\hat{r}_1(S)$‡	$\hat{r}_1(v)$‡	v (mg)	$\hat{v}$‡	$\hat{r}_1(m)$‡	ρ_w (N m^{-2})
Hesperiidae Pyrginae	Heliopetes	sp.	–	1	4.65	–	66.4	13.4	21.1	3.57	8.6	0.230	17.4	1.86	0.433	0.505	4.8	1.00	0.33	1.75
Pieridae Coliadinae	Aphrissa	boisduvalii	100	7	5.64	0.49	197.9	21.2	79.3	4.35	11.0	0.153	33.5	8.52	0.497	0.581	59.5	1.10	0.43	1.14
	Aphrissa	statira	100	15	5.80	0.48	219.2	22.7	87.3	4.60	11.8	0.183	34.3	9.69	0.488	0.573	67.3	1.11	0.44	1.11
	Phoebis	argante	82	5	5.46	1.62	235.7	22.1	94.6	4.50	10.8	0.186	35.4	10.56	0.505	0.550	76.8	1.14	0.44	1.09
	Phoebis	philea	100	2	5.13	0.11	412.3	28.3	189.1	5.82	13.8	0.162	43.4	15.39	0.505	0.589	141.5	1.15	0.45	1.30
	Phoebis	trite	100	1	5.13	–	198.4	22.9	97.3	4.60	12.4	0.142	34.5	10.45	0.514	0.660	90.3	1.11	0.45	0.93
Pierinae	Itaballia	demophoon	0†	1	2.00	–	35.8	14.8	11.4	2.60	8.4	0.226	24.6	3.91	0.476	0.470	15.4	1.13	0.58	0.45
Nymphalidae: Danainae	Danaus	gillipus	20	3	3.63	0.25	258.4	26.7	102.7	4.54	14.4	0.191	42.6	11.99	0.485	0.541	85.6	1.16	0.39	1.06
Ithomiinae	Olyras	insignis	0†	1	2.66	–	378.5	30.2	113.7	5.07	19.2	0.299	48.3	12.75	0.466	0.502	67.8	1.10	0.46	1.45
	Mechanitis	polymnia	0	1	2.66	–	75.6	21.6	21.4	2.35	15.8	0.322	30.7	4.31	0.445	0.424	12.8	1.04	0.35	0.86
	Melinaea	parallelis	3†	1	2.66	–	188.6	30.0	51.9	3.62	22.6	0.356	42.4	8.94	0.480	0.506	42.5	1.09	0.41	1.03
Nymphalinae Group I	Agraulis	vanillae	75	1	5.13	–	284.2	23.9	95.0	4.83	13.3	0.236	40.4	8.90	0.458	0.465	58.4	1.22	0.43	1.56
	Dryadula	phaetusa	88	3	3.39	0.13	274.5	27.6	100.0	4.73	16.8	0.220	43.0	12.27	0.444	0.516	72.7	1.18	0.46	1.09
	Dryas	julia	92	1	3.05	–	172.7	19.6	65.0	4.07	11.3	0.210	39.9	7.37	0.407	0.451	34.5	1.12	0.40	1.15
	Eueides	tybia	39	1	2.57	–	75.9	15.3	24.2	2.82	9.4	0.236	30.7	4.17	0.393	0.478	14.3	1.06	0.50	0.89
	Heliconius	cydno	0	1	2.09	–	140.4	25.9	53.6	3.92	16.7	0.178	39.4	8.40	0.430	0.478	37.4	1.08	0.44	0.82
	Heliconius	erato	0	2	2.12	0.09	95.7	22.7	35.6	3.41	13.5	0.165	35.6	6.91	0.463	0.458	27.9	1.09	0.38	0.68
	Heliconius	hecale	0	3	2.45	0.05	197.2	28.0	59.4	3.92	18.8	0.262	43.0	9.71	0.461	0.496	44.6	1.08	0.45	0.99
	Heliconius	sapho	0	1	2.19	–	154.9	21.9	54.4	3.92	12.8	0.211	40.1	9.41	0.457	0.543	51.6	1.10	0.44	0.81
	Heliconius	sara	0	1	2.66	–	167.5	20.7	51.8	3.73	11.4	0.242	38.0	7.31	0.458	0.496	29.1	1.07	0.44	1.12
	Philaethria	dido	100	2	2.45	0.59	223.3	23.5	81.4	4.72	12.7	0.153	49.5	11.73	0.444	0.448	66.7	1.18	0.42	0.91

Table 1. *Continued*

Family Subfamily	Genus	Species	Palatability (% eaten)	N	V (m s^{-1})	s^2	m (mg)	L (mm)	m_t (mg)	d_t (mm)	L_a (mm)	$\hat{l}_1$‡	R (mm)	S (cm^2)	$\hat{r}_1(S)$‡	$\hat{r}_1(v)$‡	v (mg)	$\hat{v}$‡	$\hat{r}_1(m)$‡ (mg)	ρ_w (N m^{-2})
Group II	*Anartia*	*fatima*	100	2	3.95	0.11	121.2	18.8	48.2	3.51	9.3	0.147	29.3	6.88	0.562	0.586	53.4	1.10	0.42	0.86
	Junonia	*evarete*	93	1	2.99	–	108.1	17.5	51.9	3.78	8.9	0.130	25.8	4.93	0.519	0.567	28.7	1.05	0.51	1.07
Group III	*Adelpha*	*iphiclus*	100	1	3.71	–	93.9	17.7	46.2	3.54	8.6	0.100	27.6	5.68	0.496	0.586	33.1	1.07	0.46	0.81
	Historis	*acheronta*	100	2	6.56	0.45	497.4	26.3	247.4	5.84	11.4	0.139	43.3	11.91	0.463	0.484	85.6	1.28	0.35	2.11
	Marpesia	*alcibiades*	100	6	4.73	0.33	142.5	17.4	61.2	4.08	7.9	0.155	32.0	6.95	0.515	0.572	53.3	1.13	0.42	1.02
	Marpesia	*petreus*	100	4	4.95	0.28	199.6	18.6	83.4	4.46	8.6	0.190	40.3	9.32	0.453	0.496	62.1	1.16	0.42	1.05
	Pyrrhogyra	*crameri*	100	1	2.37	–	112.6	15.6	37.1	3.50	8.0	0.184	27.8	6.29	0.482	0.567	28.7	1.05	0.51	0.88
Morphinae	*Morpho*	*amathonte*	100	1	2.66	–	523.3	25.7	208.9	6.33	12.1	0.177	73.5	36.88	0.511	0.530	570.0	1.30	0.37	0.70
Satyrinae	*Cissia*	sp.	100†	1	2.52	–	94.4	15.4	26.9	2.94	8.4	0.260	24.9	4.91	0.531	0.558	26.7	1.07	0.51	0.94
Papilionidae Papilioninae	*Eurytides*	*ilus**	100†	2	4.77	0.25	332.0	22.0	104.4	4.68	12.2	0.231	43.5	11.10	0.494	0.482	71.6	1.23	0.40	1.46
	Eurytides	*protesilaus*	100†	1	5.61	–	639.6	26.6	199.7	5.62	12.9	0.240	51.1	16.25	0.476	0.510	130.0	1.26	0.32	1.93
	Papilio	*thoas*	88	1	6.79	–	384.5	26.6	159.7	5.10	12.3	0.156	53.3	15.80	0.462	0.496	97.1	1.22	0.38	1.19
	Battus	*polydamas*	33	2	6.56	0.00	520.1	29.3	205.6	5.38	14.6	0.194	48.4	13.48	0.470	0.494	109.9	1.26	0.39	1.86
	Parides	*arcas*	0	2	2.76	0.16	168.9	24.9	66.4	4.15	14.8	0.213	36.7	7.21	0.418	0.468	34.6	1.19	0.40	1.14
	Parides	*sesostris*	5	1	4.42	–	306.3	28.7	123.1	4.93	17.0	0.214	42.3	11.93	0.473	0.510	75.6	1.18	0.45	1.26

*Presumed Batesian mimic.

†Palatability assumed to be equal to that of closely related species (see Chai, 1990).

‡Non-dimensionalized morphological parameters.

Features are mean values for each species, including body mass (m), body length (L), thoracic mass (m_t), thoracic diameter (d_t), abdominal length (L_a), center of body mass ($\hat{l}_1$), wing length (R), wing area (single pair, S), wing centroid [$\hat{r}_1(S)$], first moment of virtual wing mass [$\hat{r}_1(v)$], virtual wing mass and non-dimensionalized virtual wing mass (v), center of wing mass [$\hat{r}_1(m)$], and wing loading (ρ_w).

Table 2. *Summary table for a forward stepwise regression analysis (SAS version 6.0) of the dependent variable mean palatability and twelve flight-related morphological features (α=0.15 to enter or remove)*

Entered	Removed	d.f.	M.S.	F	P	Variance
Position of center of body mass		1	18384	16.4	<0.0005	39.6
Abdominal length		2	10601	2.7	0.11	45.7
Thoracic diameter		3	9287	11.5	<0.0001	60.0
	Position of center of body mass	2	9810	17.9	<0.0001	59.9
Error		24	776			

For each step, d.f., M.S., *F*, *P* and variance are presented for the cumulative model.

Table 3. *Summary table for a heirarchical general linear model (SAS version 6.0) of the dependent variable position of center of body mass on mass allocation to the thorax and abdominal length*

Factor	d.f.	M.S.	Partial F	P	Cumulative variance
Relative thoracic mass	1	0.072	69.5	<0.001	78.0
Abdominal length	1	0.005	7.4	0.01	83.0
Error	25	0.016			

Thoracic mass was adjusted for body mass using residual values of log thoracic mass plotted against log body mass.

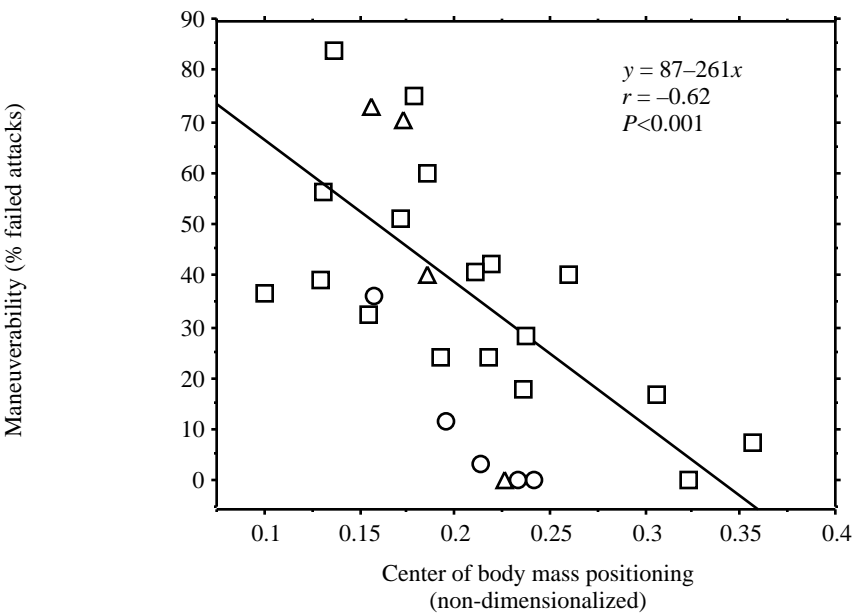
$y = 87-261x$
$r = -0.62$
$P<0.001$

Fig. 2. The proportion of failed attacks by the rufous-tailed jacamars regressed on the position of center of body mass, as a fraction of body length behind the wing base, for 27 genera of butterflies. A negative slope is observed within all three butterfly families: squares, Nymphalidae; triangles, Pieridae; circles, Papilionidae.

Table 4. *Forward stepwise regression analysis (SAS version 6.0) of the dependent variable mean airspeed and twelve flight-related morphological features ($\alpha=0.15$ to enter or remove)*

Entered	d.f.	M.S.	*F*	*P*	Variance
Wing loading	1	33.4	24.9	<0.0001	50.0
Position of center of body mass	2	21.3	21.0	<0.0001	63.6
Error	24	1.0			

For each step, d.f., M.S., *F*, *P*, and variance are presented for the cumulative model.

Supporting Ellington's (1984*a*,*b*) hypothesis that cm_{body} is relevant to insect maneuverability, it was the only significant predictor of the proportion of failed attacks by the rufous-tailed jacamar (Fig. 2, *P*<0.001). The best morphological predictors of airspeed included, in order of their contribution, wing loading and cm_{body} (Table 4).

The significance of the position of center of body mass to flight speed was not predicted by Ellington (1984*a–c*). However, mass allocation to the thorax is relevant to flight speed (Srygley and Chai, 1990*b*) and also affects the position of center of body mass. In order to assess the effect of mass allocation on variation in cm_{body}, an *a posteriori* hierarchical ANOVA was performed on the dependent variable cm_{body} with the independent variables entered in the following order: relative thoracic mass and abdominal length. Both relative thoracic mass and abdominal length are significant determinants of cm_{body} (Table 3). Mass allocation to the thorax contributes to flight speed (Srygley and Chai, 1990*b*), linear acceleration (for discussion see Marden and Chai, 1991) and presumably maneuverability of the butterflies. Above and beyond mass allocation, abdominal length explains additional variation in cm_{body} and only contributes to maneuverability.

Discussion

Our model, in which thoracic diameter and abdominal length together best predicted palatability, is very similar to that of Chai and Srygley (1990), in which body shape (i.e. thoracic diameter relative to body length) was the best predictor for palatability and explained a similar amount of variation. This congruence is probably a result of the extreme difference in abdominal length between palatable and unpalatable butterflies, which undoubtedly influences overall body length. Here, we have demonstrated that body shape, along with differences in mass allocation that are associated with it, may influence two aspects of flight performance: flight speed and maneuverability.

For a given abdominal mass, longer abdomens position cm_{body} further back from the wing base. Abdomens of palatable butterflies are typically short and squat, whereas the abdomens of distasteful butterflies are long and thin and cm_{body} is positioned more posteriorly. Indeed, the swollen terminal segments of many distasteful butterflies (e.g. danaines and ithomiines) give a clubbed shape to the abdomen and position cm_{body} extremely far from the wing base (Srygley, 1991).

The moment of rotational inertia decreases with proximity of cm_{body} to the wing base (Ellington, 1984*b*). As a result, the shortened abdomens that are characteristic of

palatable butterflies probably enhance their maneuverability. In contrast, the moment of rotational inertia increases with the elongation of the abdomen that is characteristic of distasteful butterflies. The well-known ease of capture of distasteful butterflies probably results from a reduction in maneuverability that is associated with this increase in inertia. However, it should be noted that when captured by the rufous-tailed jacamars in presentation experiments (Chai, 1990), distasteful butterflies survived grasping and were released unharmed more frequently than palatable ones.

Moreover, for a given body mass, cm_{body} is positioned nearer to the wing base for palatable butterflies because they allocate relatively more mass to the thorax (Table 3). Flight muscle mass (the majority of thoracic mass) is positively associated with the mechanical power available for flight (Ellington, 1991) and, perhaps as a result, maximum flight speed. For a sample of 47 neotropical species, mass allocation to the thorax was associated with relative flight speed (winglengths s^{-1}; Srygley and Chai, 1990b). In addition, greater mass allocation to the thorax detracts from mass allocation to the abdomen and positions cm_{body} nearer to the wing base.

Wing loading is positively correlated with flight speed in a diversity of taxa (Lighthill, 1977), including butterflies (Chai and Srygley, 1990; Dudley, 1990), whereas it is negatively associated with maneuverability (Norberg and Rayner, 1987; Pennycuick, 1989). Perhaps as a result of these conflicting selection forces, wing loading was not correlated with palatability.

In contrast to wing loading, the positive association between cm_{body} and flight speed in conjunction with the positive association between cm_{body} and maneuverability underscore the importance of this single morphological parameter to flight performance. We suggest that concerted selection is acting on mass allocation to the thorax because of its dual effects on flight speed and maneuverability.

Norberg and Rayner (1987) identified two components of maneuverability that may be subject to different selection pressures: turning radius and speed. Theoretically, the position of center of body mass will affect radial acceleration and thereby turning radius, whereas mass allocation to the thorax is likely to affect turning speed. The jacamar provides a qualitative bioassay for maneuverability that includes both of these components and forward acceleration. Further study is needed to quantify each component of butterfly maneuverability.

This research has identified the position of center of body mass as a principal correlate of palatability and natural flight speeds of tropical butterflies. Above and beyond its association with mass allocation to the thorax and consequently flight speed, the position of center of body mass is associated with abdominal length and maneuverability. Abdominal size and shape in palatable species may be more constrained than in their distasteful counterparts. However, multiple regression analysis is insufficient to prove that the position of center of body mass is under direct selection. Because of the possibility of covariance with unmeasured traits, the characters that we measured may not be selected directly. Future research will experimentally test the prediction that positional changes in cm_{body} influence maneuverability and ultimately survivorship.

For those organisms such as butterflies that possess a majority of their mass in the thoracic or abdominal regions (Srygley and Chai, 1990b; Marden and Chai, 1991), the

position of cm_{body} may serve as a single predictor of both airspeed and maneuverability. Trade-offs in mass allocation to the thorax and abdomen are likely to be general (for a review of trade-offs associated with flight, see Roff, 1986). For example, mass allocation to flight muscle in birds and bats contributes to their maximum vertical force during take-off (Marden, 1987). Mass allocation to flight muscle in the vertebrate thorax, resulting in positional changes in cm_{body}, may also enhance maneuverability. We stress that greater attention should be addressed to the position of the center of body mass in the analysis of flight for insects, birds and mammals.

References

ALEXANDER, R. M. (1982). *Animal Mechanics*. Oxford: Blackwell Scientific.

BETTS, C. R. AND WOOTTON, R. J. (1988). Wing shape and flight behaviour in butterflies (Lepidoptera: Papilionoidea and Hesperioidea): a preliminary analysis. *J. exp. Biol.* **138**, 271–288.

CHAI, P. (1990). Relationships between visual characteristics of rainforest butterflies and responses of a specialized insectivorous bird. In *Adaptive Coloration in Invertebrates. Proceedings of Symposium Sponsored by American Society of Zoologists* (ed. M. Wicksten), pp. 31–60. Galveston: Seagrant College Program, Texas A & M University.

CHAI, P. AND SRYGLEY, R. B. (1990). Predation and the flight, morphology and temperature of Neotropical rain-forest butterflies. *Am. Nat.* **135**, 748–765.

DEVRIES, P. J. AND DUDLEY, R. (1990). Morphometrics, airspeed, thermoregulation and lipid reserves of migrating *Urania fulgens* (Uraniidae) moths in natural free flight. *Physiol. Zool.* **63**, 235–251.

DUDLEY, R. (1990). Biomechanics of flight in neotropical butterflies: morphometrics and kinematics. *J. exp. Biol.* **150**, 37–53.

DUDLEY, R. (1991). Biomechanics of flight in neotropical butterflies: aerodynamics and mechanical power requirements. *J. exp. Biol.* **159**, 335–357.

DUDLEY, R. AND DEVRIES, P. J. (1990). Flight physiology of migrating *Urania fulgens* (Uraniidae) moths: kinematics and aerodynamics of natural free flight. *J. comp. Physiol.* A **167**, 145–154.

ELLINGTON, C. P. (1984*a*). The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil. Trans. R. Soc. Lond. B* **305**, 17–40.

ELLINGTON, C. P. (1984*b*). The aerodynamics of hovering insect flight. III. Kinematics. *Phil. Trans. R. Soc. Lond. B* **305**, 41–78.

ELLINGTON, C. P. (1984*c*). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. Lond. B* **305**, 145–181.

ELLINGTON, C. P. (1991). Limitations on animal flight performance. *J. exp. Biol.* **160**, 71–91.

HARVEY, P. H. AND MACE, G. M. (1982). Comparisons between taxa and adaptive trends: problems of methodology. In *Current Problems in Sociobiology* (ed. King's College Sociobiology Group), pp. 343–361. Cambridge: Cambridge University Press.

HARVEY, P. H. AND PAGEL, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

KENWARD, R. E. (1978). Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.* **47**, 449–460.

KREIGHBAUM, E. AND BARTHELS, K. M. (1981). *Biomechanics: a Qualitative Approach for Studying Human Movement*. Minneapolis, Minnesota: Burgess Publishing Co.

LIGHTHILL, M. J. (1977). Introduction to the scaling of animal locomotion. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 365–404. New York: Academic Press.

MARDEN, J. H. (1987). Maximum lift production during takeoff in flying animals. *J. exp. Biol.* **130**, 235–258.

Marden, J. H. (1989). Body building dragonflies: costs and benefits of maximizing flight muscle. *Physiol. Zool.* **62**, 505–521.

Marden, J. H. and Chai, P.(1991). Aerial predation and butterfly design: how palatability, mimicry and the need for evasive flight constrain mass allocation. *Am. Nat.* **138**, 15–36.

Norberg, U. M. (1986). Evolutionary convergence in foraging niche and flight morphology in insectivorous aerial-hawking birds and bats. *Ornis Scand.* **17**, 253–260.

Norberg, U. M. and Rayner, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* **316**, 335–427.

Pennycuick, C. J.(1989). *Bird Flight Performance.* Oxford: Oxford University Press.

Roff, D. A.(1986). The evolution of wing dimorphism in insects. *Evolution* **40**, 1009–1020.

Schmidt-Nielsen, K. (1989). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.

Srygley, R. B. (1991). The associations of palatability with flight, morphology and thermal biology of Neotropical butterflies. PhD thesis, University of Texas.

Srygley, R. B. and Chai, P. (1990*a*). Predation and the elevation of thoracic temperature in brightly colored Neotropical butterflies. *Am. Nat.* **135**, 766–787.

Srygley, R. B. and Chai, P. (1990*b*). Flight morphology of Neotropical butterflies: palatability and distribution of mass to the thorax and abdomen. *Oecologia* **84**, 491–499.