

FLIGHT PHYSIOLOGY OF NEOTROPICAL BUTTERFLIES: ALLOMETRY OF AIRSPEEDS DURING NATURAL FREE FLIGHT

ROBERT DUDLEY AND ROBERT B. SRYGLEY*

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

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Summary

Airspeed measurements during natural free flight were made on a total of 270 neotropical butterflies representing 62 species. Morphological data were obtained from the same individuals for which airspeeds had been determined. Flight speed was positively correlated with body mass, thoracic mass and wing loading. Controlling for body mass, higher wing loadings were correlated with increased flight speed. Flight speed and wing aspect ratio were negatively correlated. No consistent correlations were found between airspeed and wing length, wing area or body length. Released butterflies and butterflies encountered in natural free flight did not differ substantially in flight speed allometry. The observed scaling of flight speeds was similar to that derived for a much smaller sample of butterflies flying in an insectary, although absolute values of flight speed were approximately three times higher in natural flight and correlation coefficients of allometric regressions were typically lower. These results suggest that butterfly airspeeds under natural conditions can reasonably be predicted from morphological measurements, and that studying flight in enclosed spaces preserves the allometry of flight speeds.

Introduction

Knowledge of the airspeed of a flying animal is fundamental to any analysis of the aerodynamics and power requirements of flight. Most studies of insect aerodynamics and energetics have examined either controlled flight at set air velocities in wind tunnels (e.g. Weis-Fogh, 1956; Vogel, 1966; Dudley and Ellington, 1990; Ellington *et al.* 1990) or flight in enclosed chambers and insectaries (e.g. Ellington, 1984*a*; Ennos, 1989; Dudley, 1990). Flight speeds in the latter case can usually be determined photographically by measuring the number of body lengths travelled per unit time, provided that the flight path is nominally orthogonal to the optical axis of the camera. For insects flying in nature, however, logistical difficulties preclude direct airspeed measurements. Instead, groundspeed must be measured, to which is applied a correction for the ambient wind

*Present address: Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.

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vector. For small flying insects, however, ambient winds can frequently exceed maximum speed of flight, while spatial and temporal variation in the prevailing winds may also compromise the use of an average wind velocity determined at the location of the observer. Estimates of insect airspeeds that are derived from groundspeed measurements can therefore give misleading results. The limited data available on insect airspeeds are summarized in Johnson (1969; see also Lewis and Taylor, 1967). More recent studies on insect flight speeds in nature (e.g. Waloff, 1972; Balciunas and Knopf, 1977; Baker *et al.* 1981; see also Betts and Wootton, 1988) have relied upon indirect estimates of airspeeds from groundspeeds.

Recently, DeVries and Dudley (1990) and Dudley and DeVries (1990) devised a method for direct measurement of the airspeed of a flying insect and applied this technique to analyze flight biomechanics of a migratory uraniid moth. In this method, insects are followed in a small motorboat such that trajectories of the insect and boat are nominally parallel. A unidirectional anemometer is held laterally from the prow of the boat such that the probe is in the immediate vicinity of, and at the same height as, the flying insect. Airspeed is thus measured directly, and no assumptions concerning ambient wind are necessary. This paper presents such airspeed measurements for a variety of neotropical butterflies during free flight over Lake Gatún, Republic of Panama. Morphological data obtained for the same butterflies are used to evaluate the allometry of airspeeds under natural flight conditions. The significant correlations that ensue suggest that butterfly locomotor performance in the field may be reasonably predicted from simple morphological measurements.

Materials and methods

Butterflies and study site

Two categories of butterflies were used in this study. The first consisted of those insects encountered naturally crossing Lake Gatún, Republic of Panama. Lake Gatún is an artificial lake forming part of the Panama Canal and is surrounded by intact lowland rain forest (see Croat, 1978; Leigh *et al.* 1982, for general forest descriptions; and Huntington, 1932, for a description of the butterfly fauna of Barro Colorado Island, located in Lake Gatún). The second category consisted of butterflies either reared from pupae or captured elsewhere in Panama. These butterflies were maintained in the laboratory in net cages until taken out and released over Lake Gatún. In the hours prior to such release experiments, butterflies were fed 10% honey solution *ad libitum*. Butterfly species identifications were made following DeVries (1987). Hesperidae were tentatively identified from photographs in Lewis (1973).

The majority of airspeed measurements were made in the region of Lake Gatún directly southeast of Barro Colorado Island. Lake Gatún is an appropriate milieu within which to study flight performance, as many butterflies are typically found over lakes or the sea during migration (e.g. Williams, 1930), and in the course of our research we encountered 50 butterfly species crossing the lake naturally (see Results). Extended flights over water at this site are thus a likely occurrence for many butterflies.

Airspeed measurements

Field work was carried out during September–November 1989, May–July 1990, May–June 1991 and May–June 1992, during the rainy season (May–December in central Panama). No measurements were made during actual periods of rain. Airspeeds of butterflies encountered in natural flight were measured as follows. In the mornings when ambient wind was low, we cruised Lake Gatún in a small motorboat until a butterfly was spotted crossing the lake. The insect was followed on a parallel course until the speed of both butterfly and boat were approximately equal. The boat was then slowly drawn up laterally to the flying insect at a distance of 1–3 m. At this point, the boat speed and butterfly speed were assumed to be equal. Airspeed of the butterfly was then measured using hand-held telescoping anemometers (TSI 1640 and TSI 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 insect. At this position, the probe was exposed to moving air undisturbed by the flow field around the boat hull. Butterflies were followed for periods ranging from 1 to 10 min, over which typically three separate measurements of airspeed (range 1–5) were taken. Any butterfly that became startled or changed its flight behaviour during the measurement procedure was abandoned.

Released butterflies were typically taken to the centre of the lake, allowed to bask and then followed once free flight had been initiated. Ambient windspeed was measured immediately before the insect was freed. No release experiments were performed if ambient windspeed as measured from the boat exceeded 2 m s^{-1} (the average windspeed during measurements was 1.5 m s^{-1}). Released butterflies were followed for 1–5 min until flight directionality and speed appeared to be constant. After such a flight trajectory had been established, airspeed measurements were made as described previously. Butterflies that did not orient within 5 min were not used in flight trials.

Following measurements of airspeed, butterflies were captured with a net and the thoracic temperature of the butterfly was immediately measured. Various microclimatic data were taken, including ambient temperature, relative humidity and windspeed. The windspeed reading slightly underestimated the actual value because the boat was drifting freely while the measurement was made. Butterflies were placed in sealed glassine envelopes and were stored in an insulated bag for subsequent morphological analysis, typically within 2–3 h of capture.

Because accurate measurements of airspeed were essential in this study, we obtained factory calibrations of the anemometers twice during the course of the study period (August 1990, November 1992). In both cases, the calibration revealed that anemometer output had shifted to approximately 7% above the true value; the magnitude of this change was constant over the range of airspeeds investigated. Values for the immediately preceding field season were adjusted accordingly using linear regressions. On average, the adjustment changed values by less than 3%. Calibration errors combined with measurement imprecision in the field result in airspeed uncertainties between 5 and 10% of the recorded values. This variability is comparable to the airspeed variance of individual butterflies (see Results).

Table 1. Airspeed and morphological data for the species studied

ID	Family	Subfamily	Genus and species	N(n)	V	V _{max}	m	\hat{m}_t	\hat{m}_w	R	\mathcal{R}	p _w	\hat{L}	\hat{d}
1	Papilionidae:	Papilioninae	<i>Battus polydamas</i> (Linnaeus)	3(3)	5.8	6.1	551	0.38	0.086	49.6	3.54	1.89	0.59	0.16
2			<i>Euryides dolicaon</i> (Cramer)	1(0)	4.5	4.8	433	0.45	0.125	47.7	3.10	1.44	0.57	0.16
3			<i>Euryides ilus</i> (Fabricius)	3(2)	4.5	4.7	331	0.31	0.091	43.3	3.42	1.47	0.51	0.19
4			<i>Euryides protesilaus</i> (Rothschild and Jordan)	3(2)	5.3	5.5	521	0.40	0.106	51.0	3.49	1.83	0.52	0.18
5			<i>Papilio anchisiades</i> (Fabricius)	2(2)	4.6	4.7	484	0.39	0.115	54.1	3.48	1.33	0.55	0.14
6			<i>Papilio thoas</i> Rothschild and Jordan	6(3)	4.6	4.9	489	0.41	0.140	59.5	3.40	1.17	0.48	0.16
7			<i>Parides arcas</i> (Bates)	3(0)	2.9	2.9	178	0.38	0.122	37.3	3.72	1.16	0.70	0.11
8			<i>Parides sesostris</i> (Gray)	2(0)	3.1	3.2	343	0.36	0.123	42.9	3.01	1.28	0.70	0.12
9	Pieridae:	Coliadinae	<i>Aphrissa boisduvallii</i> (Felder)	29(29)	5.1	5.3	194	0.41	0.116	33.4	2.53	1.07	0.63	0.15
10			<i>Aphrissa statira</i> (Cramer)	36(36)	5.3	5.5	204	0.42	0.125	33.9	2.44	1.06	0.67	0.14
11			<i>Eurema proterpia</i> (Fabricius)	1(0)	2.9	3.3	44	0.34	0.150	21.6	2.23	0.52	0.84	0.09
12			<i>Phoebis argante</i> (Fabricius)	18(18)	4.9	5.0	227	0.43	0.132	36.0	2.33	1.00	0.64	0.15
13			<i>Phoebis philea</i> (Linnaeus)	6(6)	4.9	5.1	442	0.46	0.143	44.1	2.39	1.31	0.65	0.15
14			<i>Phoebis sennae</i> (Linnaeus)	3(3)	6.2	6.5	361	0.48	0.148	41.4	2.54	1.42	0.62	0.18
15			<i>Phoebis trite</i> (Linnaeus)	2(2)	4.8	4.8	180	0.50	0.148	33.8	2.31	0.88	0.65	0.14
16			<i>Appias drusilla</i> (Cramer)	5(5)	4.0	4.1	122	0.46	0.118	32.5	2.63	0.74	0.59	0.14
17	Pierinae		<i>Itaballia demophile</i> Joicey and Talbot	3(1)	2.7	2.7	110	0.23	0.075	26.8	2.81	0.74	0.62	0.13
18			<i>Itaballia pandosia</i> Reakirt	2(2)	2.2	2.3	50	0.38	0.133	25.2	2.82	0.53	0.67	0.11
19			<i>Metete florinda</i> (Butler)	1(0)	1.8	2.1	94	0.41	0.160	34.9	3.25	0.61	0.59	0.11
20			Nymphalidae:	Charaxinae	<i>Archaeoprepona demophon</i> Fruhstorfer	1(1)	7.0	7.2	1120	0.37	0.099	57.6	2.77	2.29
21	Danaeinae	<i>Danaus eresimus</i> Talbot			2(2)	3.9	4.1	280	0.38	0.117	42.3	3.13	1.19	0.61
22	Heliconiinae		<i>Danaus gilippus</i> Bates	4(3)	3.6	3.8	259	0.39	0.123	42.5	3.04	1.07	0.62	0.13
23			<i>Agraulis vanillae</i> (Linnaeus)	1(1)	5.0	5.1	284	0.33	0.076	40.4	3.67	1.56	0.59	0.16
24			<i>Dione juno</i> (Cramer)	3(2)	3.8	4.0	207	0.36	0.099	38.9	3.99	1.47	0.58	0.15
25			<i>Dryadula phaetusa</i> (Linnaeus)	8(3)	3.7	3.9	250	0.36	0.114	42.2	3.11	1.06	0.64	0.12
26			<i>Dryas iulia</i> (Fabricius)	5(3)	4.5	4.6	195	0.38	0.101	40.8	3.84	1.09	0.53	0.15
27			<i>Eueides lybia</i> Staudinger	1(0)	2.3	2.6	87	0.28	0.094	30.7	4.52	1.03	0.50	0.16
28			<i>Heliconius charitonius</i> (Linnaeus)	1(1)	2.3	2.8	114	0.36	0.128	42.3	4.19	0.65	0.55	0.10
29			<i>Heliconius cydno</i> Bates	1(0)	1.9	2.1	136	0.39	0.121	39.4	3.70	0.79	0.66	0.10
30	<i>Heliconius eleuchia</i> Hewitson	1(1)	3.3	3.5	189	0.36	0.122	42.4	3.37	0.87	0.56	0.13		
31	<i>Heliconius erato</i> Doubleday	3(0)	1.7	1.9	106	0.33	0.109	35.4	3.63	0.75	0.65	0.10		
32	<i>Heliconius hecale</i> Hewitson	7(1)	2.1	2.2	224	0.27	0.100	43.4	3.78	1.02	0.67	0.10		

Table 1. *Continued*

33		<i>Heliconius melpomene</i> Boisduval	1(1)	2.6	2.7	108	0.39	0.134	35.4	3.83	0.80	0.67	0.10
34		<i>Heliconius sapho</i> Doubleday	1(0)	2.0	2.2	168	0.32	0.101	40.1	3.42	0.88	0.55	0.13
35		<i>Heliconius sara</i> Stichel	7(7)	2.7	2.8	133	0.33	0.110	36.3	3.76	0.92	0.54	0.14
36		<i>Laparus doris</i> (Linnaeus)	1(0)	1.7	1.8	131	0.42	0.131	38.2	3.89	0.86	0.57	0.12
37		<i>Phlaethria dido</i> (Linnaeus)	5(1)	2.5	2.6	234	0.36	0.142	49.1	4.04	0.95	0.49	0.14
38	Ithomiinae	<i>Mechanitis lysimnia</i> Bates	1(1)	0.7	0.7	83	0.28	0.109	32.0	4.51	0.89	0.66	0.10
39		<i>Mechanitis polymnia</i> Bates	1(1)	2.5	2.7	76	0.28	0.087	30.7	4.38	0.86	0.70	0.09
40		<i>Melinaea parallela</i> (Butler)	2(1)	2.5	2.6	203	0.33	0.100	42.9	4.07	1.10	0.73	0.09
41		<i>Melinaea scylax</i> Salvin	1(1)	3.4	3.6	161	0.32	0.118	39.5	3.79	0.96	0.75	0.08
42		<i>Olyras insignis</i> Salvin	1(0)	2.5	2.7	382	0.30	0.082	48.3	3.65	1.47	0.63	0.13
43	Morphinae	<i>Morpho amathonte</i> Deyrolle	1(0)	2.6	2.7	523	0.40	0.176	73.5	2.93	0.70	0.35	0.19
44	Nymphalinae	<i>Adelpha iphicles</i> (Linnaeus)	1(1)	3.6	3.7	94	0.49	0.128	27.6	2.68	0.81	0.64	0.14
45		<i>Anartia fatima</i> Godart	7(7)	3.6	3.7	115	0.42	0.110	29.1	2.44	0.81	0.62	0.15
46		<i>Eunica alcmena</i> (Druce)	1(1)	3.0	3.5	216	0.44	0.107	35.3	2.54	1.08	0.56	0.18
47		<i>Eunica</i> sp.	1(1)	4.8	4.8	157	0.54	0.102	31.4	2.76	1.08	0.58	0.17
48		<i>Hamadryas feronia</i> (Fruhstorfer)	3(1)	4.4	4.5	315	0.47	0.124	38.3	2.58	1.32	0.65	0.16
49		<i>Hamadryas iphime</i> (Bates)	1(1)	4.5	4.8	272	0.38	0.080	35.6	3.40	1.78	0.60	0.18
50		<i>Historis acheronta</i> (Fabricius)	11(11)	6.5	6.7	533	0.49	0.089	43.3	3.21	2.24	0.60	0.19
51		<i>Junonia evarete</i> (Cramer)	2(0)	2.3	2.5	126	0.40	0.095	27.0	2.64	1.12	0.69	0.15
52		<i>Marpesia chiron</i> (Fabricius)	23(23)	4.6	4.8	144	0.41	0.116	31.4	2.93	1.04	0.54	0.19
53		<i>Marpesia petreus</i> (Cramer)	13(13)	4.9	5.1	197	0.42	0.092	39.7	3.51	1.07	0.47	0.19
54		<i>Pyrrhogyra crameri</i> Aurivillius	1(0)	2.2	2.4	113	0.33	0.099	27.8	2.46	0.88	0.56	0.19
55		<i>Pyrrhogyra neaerea</i> Godman and Salvin	1(1)	1.8	2.0	122	0.44	0.116	31.8	2.78	0.82	0.54	0.17
56		<i>Pyrrhogyra otolais</i> Bates	1(1)	3.6	3.6	124	0.45	0.129	31.9	2.35	0.70	0.50	0.19
57		<i>Siproeta stelenes</i> (Fruhstorfer)	2(1)	3.7	3.8	209	0.52	0.149	42.1	2.89	0.83	0.47	0.18
58	Satyriinae	<i>Cissia</i> sp.	1(0)	2.2	2.5	97	0.28	0.093	24.9	2.53	0.97	0.62	0.17
Hesperiidae:													
59	Hesperiinae	<i>Calpodus ethlius</i> Stoll	2(2)	7.5	7.8	256	0.52	0.041	24.9	4.72	4.77	0.82	0.19
60	Pyrginae	<i>Cycloxemia anastomosis</i> Mabille	1(1)	5.7	5.7	120	0.41	0.060	23.7	3.35	1.76	0.68	0.18
61		<i>Heliopterus</i> sp.	2(2)	4.1	4.5	74	0.38	0.052	19.3	3.55	1.71	0.70	0.18
62		<i>Typhedanus undulatus</i> (Hewitson)	1(1)	7.4	7.9	234	0.46	0.046	24.1	2.98	2.96	0.72	0.23

ID, identification number; $N(n)$, total sample size (sample size of individuals crossing Lake Gatún naturally); V , mean airspeed (m s^{-1}); V_{max} , mean maximum airspeed (m s^{-1}); m , mean body mass (mg); \hat{m}_t , mean relative thoracic mass; \hat{m}_w , mean relative wing mass; R , mean relative wing length (mm); \mathcal{R} , mean aspect ratio; P_w , mean wing loading ($N \text{ m}^{-2}$); \bar{L} , mean non-dimensional body length; \hat{d} , non-dimensional mean body diameter.

Morphological measurements

For each captured butterfly, wing length R and body length L were determined with dial calipers to the nearest 0.1 mm. The masses of the body, thorax (shorn of the legs) and one wing pair were then determined with a digital balance (Mettler AE163, accuracy ± 0.1 mg). Body mass m includes the mass of both wing pairs, m_w . Relative thoracic mass \hat{m}_t and relative wing mass \hat{m}_w were expressed as a fraction of total body mass. A mean body diameter \hat{d} was calculated assuming a mean tissue density of 1100 kg m^{-3} . The area of one wing pair, with the fore- and hindwings overlapped in a natural configuration, was measured to the nearest square millimeter using a digital leaf area meter (Delta-T Devices). The total sustaining wing area S is twice the value of a single wing pair. Wing loading $p_w (=mg/S)$ and aspect ratio $\mathcal{A} (=4R^2/S)$ were calculated for each butterfly. Mean values of morphological variables were determined for each species.

Reduced major axis (RMA) correlations upon log-transformed variables (see Rayner, 1985) were used to evaluate the allometric dependence of airspeed upon the aforementioned morphological variables. All statistical analyses were performed on the total sample of butterflies as well as on subsets of released butterflies and those butterflies encountered in natural flight over the lake.

Results*Flight behaviour*

The majority of butterflies encountered in natural flight engaged in continuous flapping flight at heights of 0.5–1.5 m above the surface of the lake. Gliding was only rarely performed, was typically very steep, and seemed to occur only when the butterfly had risen higher than normal for the species above the lake surface. Airspeeds and orientations of butterflies naturally crossing the lake were remarkably constant. Of those butterflies taken out and released on the lake, some immediately flew upwards and were lost, while others exhibited disoriented flight for periods of minutes before finally establishing a regular trajectory. Most released butterflies were, however, capable of sustained flight for extended periods (>5 min), with flight path oscillations and flight styles similar to those of conspecifics flying naturally in the wild (R. Dudley and R. B. Srygley, personal observation).

Complete airspeed and morphological data were obtained for 270 butterflies (Table 1). This sample represented a total of 62 species from 12 subfamilies. A total of 213 butterflies representing 50 species were encountered in natural flight over Lake Gatún. Coefficients of variation for mean airspeeds of individuals were low, averaging 6% (range 0–28%). Twenty-seven species were represented by only one individual. Of those species represented by more than one individual, coefficients of variation for mean species airspeed were somewhat higher, averaging 0.21 (range 0.0–0.66).

Airspeed allometry

Allometric relationships between airspeed and morphological variables for all butterflies are given in Table 2. Airspeed was positively correlated with body mass (Fig. 1), thoracic mass, mean body diameter and wing loading (Fig. 2). Airspeed was

Table 2. Predicted and empirical allometry between mean forward airspeed V and eight morphological variables for 62 neotropical butterfly species

Variable	Expected scaling	Equation for V	95 % lower CL	95 % upper CL	r	P
Mass	1/6	$V = 8.7m^{0.56*}$	0.44	0.72	0.75	0.0001
Thoracic mass	1/6	$V = 17.6m_t^{0.63*}$	0.46	0.86	0.81	0.0001
Wing length	1/2	$V = 0.01R^{1.73}$	–	–	0.32	0.42 (NS)
Wing area	1/4	$V = 886.9S^{0.87}$	–	–	0.45	0.13 (NS)
Body length	1/2	$V = 0.01L^{2.08}$	–	–	0.37	0.28 (NS)
Mean body diameter	1/2	$V = 113.9d^{1.81*}$	1.26	2.59	0.77	0.0001
Aspect ratio	0	$V = 46.9AR^{-2.27*}$	-11.59	-0.44	0.52	0.035
Wing loading	1/2	$V = 3.1p_w^{1.11*}$	0.82	1.50	0.81	0.0001

Expected scaling is predicted from aerodynamic theory (see Norberg and Rayner, 1987); 95 % lower and upper CL refer to the confidence limits for the allometric exponent ($\alpha=0.05$).

All equations were determined using RMA correlations of log-transformed data; units are grams, millimeters or seconds. Significant differences from isometric scaling are indicated with an asterisk; NS indicates no significant difference.

negatively correlated with aspect ratio (Fig. 3). Slopes of the regressions relating airspeed to morphological variables differed significantly from those predicted assuming isometric design (Norberg and Rayner, 1987; see Table 2). No correlation was found between airspeed and body length, wing length or wing area (Table 2). The negative regression of

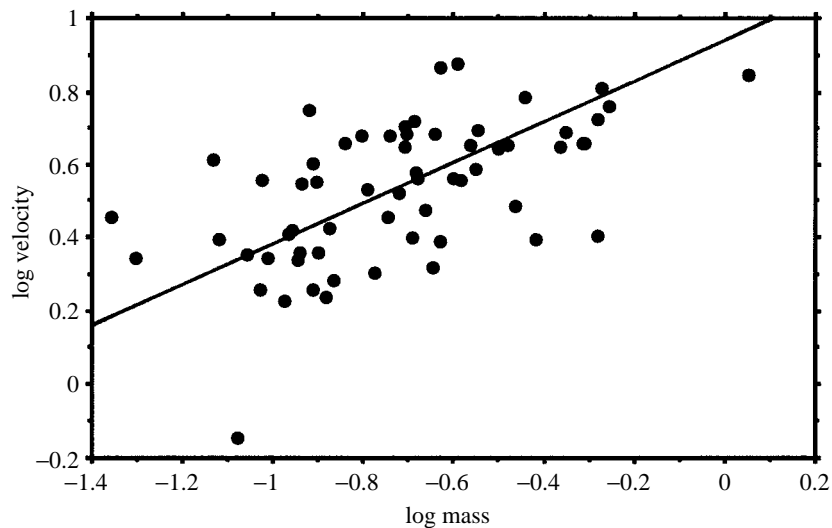


Fig. 1. Airspeed V ($m s^{-1}$) plotted against body mass m (g) for 62 butterfly species in free flight over Lake Gatún, Republic of Panama. The equation for the RMA correlation is listed in Table 2. The 95 % confidence limits of the slope exclude the value (0.166) predicted by isometry and biomechanical considerations, but include the value (0.378) derived by Dudley (1990) for fifteen neotropical butterflies flying in an insectary. The outlier in the bottom left of the figure (see also Fig. 2) is an ithomiine nymphalid (no. 38).

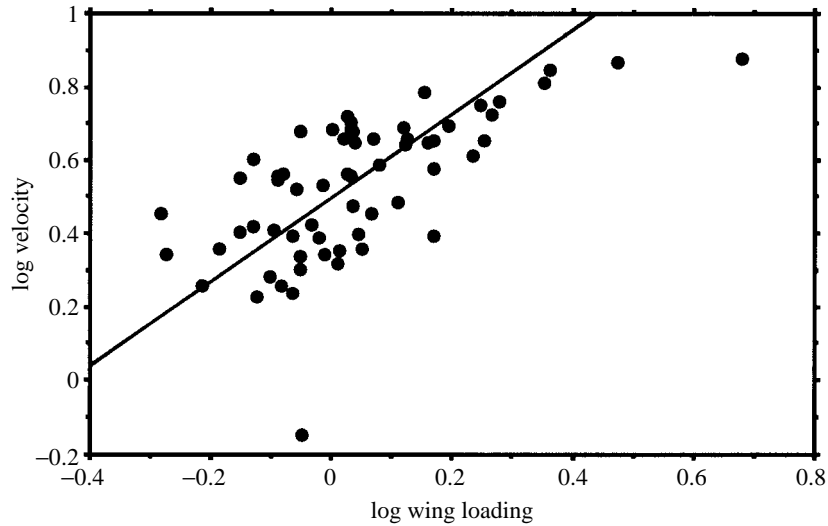


Fig. 2. Airspeed V (m s^{-1}) plotted against wing loading p_w (N m^{-2}) for the same butterfly species as in Fig. 1. The equation of the RMA correlation is listed in Table 2. The allometric dependence of V upon p_w is significantly different from isometry and, like that of body mass, does not differ significantly from the value (0.848) derived by Dudley (1990).

airspeed with aspect ratio is no longer significant if the bottom outlier (no. 38, Table 1) is removed. However, if the other outlier at the highest aspect ratio (no. 62) is removed, the regression is weakly significant ($r=0.28$, $P<0.05$).

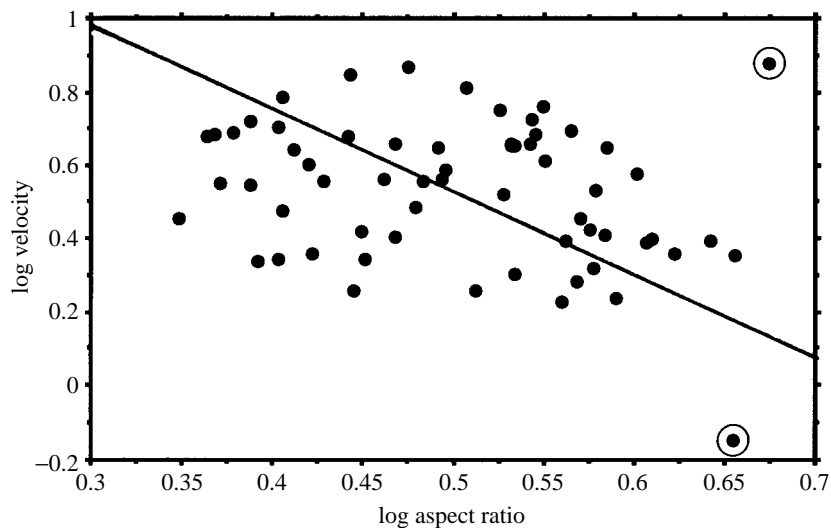


Fig. 3. Airspeed V (m s^{-1}) plotted against mean wing aspect ratio \mathcal{A} for the butterfly species of Figs 1 and 2. The equation of the RMA correlation is listed in Table 2. Airspeeds show a slight but significant tendency to decrease with increased aspect ratio. The two circled outliers are referred to in the text.

Comparing the subset of butterflies intercepted while naturally crossing the lake with the subset of those that were released, allometric relationships relating airspeed to morphological variables were generally equivalent between the two groups. The only difference was that the log–log regression relating mean airspeed and wing area was significant ($P < 0.05$) for butterflies intercepted in natural flight, but not for released butterflies. For all other allometric regressions, slopes for released butterflies were within the 95% confidence intervals determined for the set of butterflies intercepted in natural flight. Thus, overall free-flight allometry of released and naturally flying butterflies did not differ substantially.

To test the possibility that airspeed and wing loading were positively correlated when controlling for variation in body mass, standardized residual deviations were determined from interspecific log–log regressions of airspeed on mass and of wing loading on mass. These residual deviations were positively correlated with each other ($r = 0.48$, $P < 0.001$), suggesting that, at equivalent body masses, species with greater wing loadings tended to fly faster. Interspecifically, mean maximum airspeeds were positively correlated with mean airspeed ($r = 0.997$, $P < 0.0001$) and exceeded the mean airspeed by 5% on average. Allometric relationships determined using mean maximum airspeeds did not differ significantly from those calculated using average values. The fastest butterfly studied was a pyrgine hesperiid (no. 62) flying at 7.9 m s^{-1} , while an ithomiine nymphalid (no. 38) was the slowest at just 0.7 m s^{-1} .

Using the data of Table 1, an interspecific allometric analysis of wing morphology showed no correlation of aspect ratio with body mass (log–log linear regression; $R \propto m^{-0.002}$, $r = 0.01$, $P > 0.95$), while wing area and wing loading exhibited positive allometry (log–log RMA regressions; $S \propto m^{0.79}$, $r = 0.78$, $P < 0.001$, and $p_w \propto m^{0.62}$, $r = 0.61$, $P < 0.001$, respectively).

Comparative analyses are often confounded by similarities arising from common descent (Harvey and Pagel, 1991). Nested analysis of variance in airspeeds revealed that the lowest taxonomic level of significance was the genus (see Srygley and Dudley, 1993), but the preceding allometric analysis was explicitly intended to elucidate biomechanical differences between species. Whereas the allometric results presented here are intended for comparison with aerodynamic predictions applicable to flying machines independent of their historical origin, it is of interest to consider taxonomic subsamples from the full data set to see whether the ensuing allometric patterns are equivalent to the overall interspecific analysis. Interfamilial variation was not examined here because the sample size of families was small ($N = 4$). However, two subfamilies with high generic sample sizes (Heliconiinae, Nymphalinae) were analyzed for allometric scaling of flight speed within a subfamily. In contrast to the negative correlation of the full data set (Fig. 3), airspeed within the two subfamilies was independent of aspect ratio ($P > 0.05$ in both cases). However, airspeeds within the Heliconiinae and Nymphalinae showed significant positive allometry with respect to body mass (log–log RMA regressions; $V \propto m^{0.93}$, $r = 0.64$, $P < 0.05$, and $V \propto m^{0.73}$, $r = 0.64$, $P < 0.05$, respectively) and with respect to wing loading ($V \propto p_w^{1.11}$, $r = 0.57$, $P < 0.05$, and $V \propto p_w^{1.47}$, $r = 0.73$, $P < 0.01$, respectively). Allometric RMA slopes of the body mass and wing loading equations (Table 2) did not differ significantly between the two subfamilies, nor from those exponents derived for the

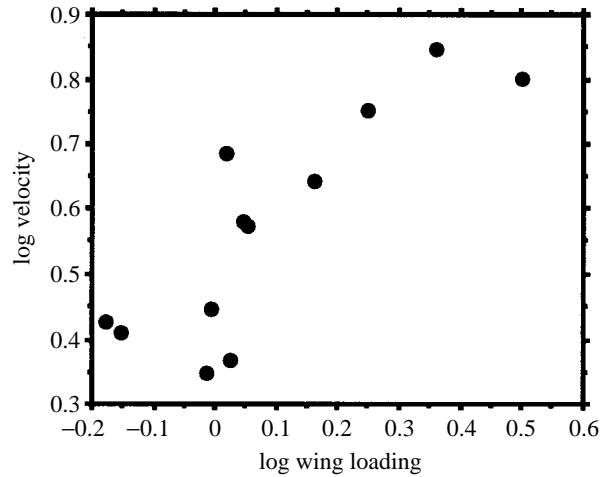


Fig. 4. Airspeed V (m s^{-1}) plotted against wing loading p_w (N m^{-2}) for 12 butterfly subfamilies. See text for RMA regression. Allometry of airspeeds using mean values for the subfamilies does not differ significantly from that determined interspecifically (Fig. 2).

full species set. In summary, analysis within two subfamilies results in loss of the negative allometry between airspeed and aspect ratio that characterizes the full data set. This difference may result from much reduced sample sizes in the former case. However, the allometric variations of airspeed with body mass and wing loading are the same as those for the full data set.

Comparing mean airspeeds and morphological data among butterfly subfamilies, the two hesperiid subfamilies (Hesperiinae, Pyrginae) and the charaxine nymphalid were the fastest-flying insects (Table 3). Interestingly, an order of magnitude variation in body mass is apparent in this comparison. It must be noted that sample sizes for subfamilies are

Table 3. Mean airspeeds V (m s^{-1}), sample size N , body mass m (g), aspect ratio \mathcal{A} and wing loading p_w (N m^{-2}) for the twelve butterfly subfamilies described in Table 1

Subfamily	N^*	V	m	\mathcal{A}	p_w
Papilioninae	8	4.4	0.416	3.39	1.45
Coliadinae	7	4.9	0.236	2.40	1.04
Pierinae	4	2.7	0.094	2.88	0.66
Charaxinae	1	7.1	1.120	2.77	2.29
Danainae	2	3.8	0.269	3.08	1.13
Heliconiinae	15	2.8	0.171	3.78	0.98
Ithomiinae	5	2.3	0.181	4.08	1.06
Morphinae	1	2.6	0.523	2.93	0.70
Nymphalinae	14	3.8	0.195	2.80	1.11
Satyrinae	1	2.2	0.097	2.53	0.97
Hesperiinae	1	5.7	0.120	3.35	1.76
Pyrginae	3	6.4	0.188	3.75	3.15

*Number of species sampled within each subfamily.

highly uneven. Using the data of Table 3, no significant allometric relationships were found between airspeed and body mass or between airspeed and wing aspect ratio ($r=0.43$, $P>0.15$, and $r=0.04$, $P>0.91$, respectively), while flight speed and wing loading were highly correlated (log–log RMA regression, $p_w \propto m^{0.88}$, $r=0.84$, $P<0.001$; see Fig. 4). The latter allometric exponent fell within the 95% confidence intervals for the interspecific regression relating flight speed and wing loading (Fig. 2; Table 2).

Discussion

Individual and intraspecific variability in butterfly airspeeds was low compared with the range of interspecific variation. The relative constancy of airspeeds for butterflies in natural flight (and also for released insects) suggests that experimenter presence is not adversely influencing flight performance. Flight of released butterflies once a nominal equilibrium has been established is a reasonable analogue for studying natural flight behaviour, although flight performance may be somewhat diminished. The present sample sizes are too small to conduct a detailed analysis of the effects of release on flight speed selection, but in thirteen species for which both natural and release airspeeds were available, airspeeds of released individuals were significantly lower than those of their naturally flying counterparts (Wilcoxon signed-rank test, $t=13$, $P<0.01$). This comparison of individual butterflies within a species does not control for morphological differences or for possibly varying microclimatic conditions during flight. No significant differences existed between free and released butterflies in either ambient temperature or shortwave radiation at time of capture (Wilcoxon signed-rank test, $P>0.05$). Released butterflies did, however, manifest significantly lower thoracic temperatures ($\Delta T_{th} = -2.2^\circ\text{C}$, Wilcoxon signed-rank test, $t=15$, $P<0.05$). If airspeeds could be measured on butterflies encountered in natural flight, followed by capture, subsequent release and then remeasurement of airspeed, the consequences of release methodology for flight speed selection of individual butterflies could be determined directly.

For nine of the butterfly species studied here (nos 1, 6, 9, 17, 20, 26, 43, 55 and 57; Table 1), airspeeds measured in nature are approximately three times higher on average than airspeeds estimated for the same species flying in an insectary (see Dudley, 1990; Srygley and Dudley, 1993). However, the allometric dependence of airspeed upon morphological variables is very similar (Table 2; cf. Table 5 in Dudley, 1990). Correlation coefficients for allometric regressions of natural free flight (Table 2) are much lower than those for insectary flight. This result may simply reflect the wider taxonomic range of butterflies used in the present study. Absolute airspeeds increase in natural free flight, but the allometry of flight speed appears to be unchanged across a spatial shift from insectary to lake flight. Different butterflies may thus respond similarly in terms of flight speed selection relative to perceived available space. Measurement of airspeeds on individual butterflies flying in insectaries of different sizes, and in natural flight when released across the lake, would test this hypothesis.

The positive allometry of airspeeds in butterflies (both in interspecific comparisons and within subfamilies) most probably reflects non-isometric aspects of morphological design. Wing loading exhibited positive allometry (see also Dudley, 1990; Chai and

Srygley, 1990; Srygley and Dudley, 1993). In general, reduced relative wing area requires wing velocities and, by implication, increased flight speed to compensate for aerodynamic force production during forward flight. The weak inverse relationship between flight speed and aspect ratio (Fig. 3) was not found for a smaller sample of butterflies flying in insectaries (Dudley, 1990) or in comparisons of flight speed and aspect ratio within the Heliconiinae and Nymphalinae. However, a negative association between aspect ratio and a measure of mean flight speed in two dimensions was found by Chai and Srygley (1990) for a sample of neotropical butterflies. No specific prediction exists on aerodynamic grounds for the scaling of aspect ratio (Norberg and Rayner, 1987). It is noteworthy that the decrease in airspeed over the range of aspect ratios considered in the present study is not dramatic and is highly sensitive to the presence of two outlier species (Fig. 2). In contrast to butterflies, bats demonstrate a positive correlation between flight speed and wing aspect ratio (Norberg and Rayner, 1987).

Flight speed selection has important consequences for mechanical power expenditure. Early models of mechanical power requirements of flying animals (e.g. Pennycuik, 1975) suggested a sharp increase in power expenditure at higher airspeeds. For most vertebrates and for bumblebees, however, power requirements are fairly constant at hovering and lower airspeeds, and then increase sharply (Ellington, 1991). In general, shapes of power curves are not known for insects with low wingbeat frequencies. Dudley and DeVries (1990) suggested for a migratory moth that the power requirements of flight increased sharply with forward airspeed, primarily as the result of an increase in profile power requirements at higher airspeeds. Because Lepidoptera generally have low wingbeat frequencies, advance ratios (the ratio of forward to flapping velocity; see Ellington, 1984a) are high, often in excess of one even at low flight velocities (see Dudley, 1990). Wing and body forces will be dominated by the forward velocity vector, so that airspeed exerts a significant effect on the summed power curve. Wing profile power is proportional to the cube of wing relative velocity (the vector sum of the induced, forward and flapping velocities), and it is likely that for all butterflies this component of total power increases sharply with forward airspeed. Parasite power (the power required to overcome drag forces) is similarly proportional to the cube of forward airspeed.

Because of these relationships between power and airspeed for insects with low wingbeat frequencies, estimates of power expenditure for butterflies in natural free flight (and particularly at high airspeeds) are of interest. Full kinematic data are not available for those butterflies studied here, but parasite and profile power can be approximated. The following calculations are made using the mean species data for the papilionid *Eurytides protesilaus*, a representative fast-flying butterfly (no. 4, Table 1). Parasite power equals the product of the projected cross-sectional area (here based on the mean body diameter), a parasite drag coefficient, air density (assumed to be 1.23 kg m^{-3}) and the cube of forward airspeed. In field flight, the longitudinal body axis of butterflies flying at airspeeds above $3\text{--}4 \text{ m s}^{-1}$ uniformly appeared to be horizontal. A body drag coefficient of 0.4 at a Reynolds number of about 9000 and a body angle of 0° (see Dudley and Ellington, 1990) can therefore be assumed. At a mean airspeed of 5.3 m s^{-1} , parasite power will then equal 8.9 W kg^{-1} in *E. protesilaus*.

A minimum estimate for profile power is determined from the total wing surface area, a

profile drag coefficient, fluid density and the cube of the forward airspeed. A profile drag coefficient of 0.7 is assumed at a Reynolds number of 9600 (see Ellington, 1984*b*). The minimum profile power for *E. protesi* would then be approximately 34.8 W kg^{-1} ; actual values will increase as a result of inclusion of the smaller flapping and induced velocities. Conservatively ignoring induced drag (which is in any event small at high velocities) and inertial power, a minimum estimate for power expenditure in *E. protesi* is about 44 W kg^{-1} , substantially in excess of values estimated for butterflies flying in an insectary at speeds of $1\text{--}3 \text{ m s}^{-1}$ (mean of 12.5 W kg^{-1} , assuming perfect elastic energy storage; see Dudley, 1991). At speeds in excess of 5 m s^{-1} , power expenditure in butterflies is similar to that for bumblebees in forward flight (see Dudley and Ellington, 1990), and any advantage of reduced wing loadings and the concomitant decrease in induced power requirements will not be realized. This estimate for a fast-flying butterfly is also similar to those made for the moth *Urania fulgens* at high airspeeds (i.e. 31 W kg^{-1} at 4 m s^{-1} ; see Dudley and DeVries, 1990). Many butterflies fly faster than 5 m s^{-1} in nature (see Table 1), and such flight is likely to be energetically expensive. Additional thoracic musculature to provide the requisite power for flight is likely in those butterflies that exceed airspeeds of 6 m s^{-1} (see nos 50, 59 and 62). Also, energetic expenditure will further increase if erratic flight paths are maintained (Dudley, 1991). A detailed kinematic and aerodynamic analysis of fast forward flight in butterflies would be required to verify these initial estimates. In general, however, it is probable that butterflies (all of which possess synchronous flight muscle) will match, at high airspeeds, the power output of asynchronous insect fliers.

Selection of flight speed within and among species will depend on a variety of behavioural, ecological and phylogenetic factors. Natural flight speeds of neotropical butterflies are correlated with palatability to an avian insectivore (Chai and Srygley, 1990; Srygley and Dudley, 1993) and may also be affected by gender, microclimate and migratory condition. These potential factors are under investigation. Ten of the species studied here (nos 9, 10, 12, 13, 14, 15, 16, 50, 52 and 53) were migrating when airspeed measurements were made. Because of the small and variable sample sizes per species, no attempt was made here to assess the magnitude of these different factors for flight speed selection. It is nonetheless striking that, in spite of such wide variance, strong allometric relationships between flight speed and morphological variables emerge from the data set (Table 2). Using release experiments, the systematic control of the aforementioned factors to assess the consequences for flight speed selection would be possible. Flight over bodies of water could also provide a useful context for assessing limits to butterfly flight performance.

The biomechanics of insect flight is most often studied on insects in enclosures or wind tunnels, but the relationship of such studies to flight in natural environments is unknown. Use of the procedures implemented herein can provide the requisite data for a comparison of laboratory and field assessments of flight performance. It is now experimentally tractable to carry out detailed surveys of insect flight under natural conditions, obtaining repeated measurements of both airspeed and morphological data on individual insects. A movie or video camera can also be used to obtain wing kinematics concurrently with airspeed measurements (see Dudley and DeVries, 1990), contributing values of such

variables as wingbeat frequency and stroke amplitude for use in aerodynamic analyses of flight. In addition to studying insects encountered in natural flight, these techniques can also be used to study insects that are released over bodies of water. Airspeeds and wing kinematics can easily be determined on such released insects if regular flight trajectories are established. Given the paucity of data on insect flight performance in nature, airspeed measurements and kinematic analyses of free flight in additional insect taxa are now warranted.

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