Airspeed adjustment and lipid reserves in migratory Neotropical butterflies

R. Dudley[1,2,*] and R. B. Srygley[2,3],†

[1]*Department of Integrative Biology, University of California, Berkeley, CA 94720, USA;* [2]*Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama; and* [3]*Department of Zoology, Oxford University, Oxford, UK*

Summary

1. Aerodynamic theory predicts that migrant fliers should reduce their speed of flight as endogenous energy reserves are gradually consumed. This prediction was tested for butterfly species (Pieridae and Nymphalidae) that engage in annual rainy season migrations through central Panama.

2. Direct airspeed measurements were made on butterflies in natural free flight, followed by chloroform : methanol extractions of abdominal lipids from the same insects.

3. Among individuals within particular species/gender subsets, airspeeds during flight were higher with greater lipid content following adjustment for body mass. Although it was not possible to measure lipid content repeatedly on a single insect, these comparisons among individuals for five migratory species suggest that butterflies reduce their flight speed as lipid reserves are progressively depleted.

4. Because choice of airspeed can strongly influence the rate of energetic expenditure, these results together with previously described strategies of wind drift compensation in the same taxa demonstrate sophisticated long-distance orientation and optimization strategies by migratory Neotropical butterflies flying within the boundary layer.

Key-words: Central America, flight velocity, insect flight, Nymphalidae, optimal migration, Panama, Pieridae

Introduction

Migration by flight requires that animals negotiate aerial landscapes of varying wind speeds and directions, for which orientational mechanisms and regular course correction are required. In addition to such external perturbations of the flight trajectory, oxidation of endogenous reserves may induce compensatory changes in flight speed if migratory distances are to be maximized. The depletion of lipids over long distances can substantially reduce body mass and thereby reduce the instantaneous cost of flight as well as the airspeed associated with maximizing migratory range (Pennycuick 1969, 1978). In particular, flight speed is predicted to vary in direct proportion to the square root of body mass if individuals are maximizing the distance travelled per unit energy expended for an invariant wing morphology. Migrating brent geese (*Brenta bernicla*), for example, fly more slowly in autumn relative to spring in accordance with their associated change in body mass between the two seasons (Green & Alterstam

2000). For many long-distance insect migrants, the occurrence of substantial premigratory lipid loading (Johnson 1969) suggests that a comparable strategy would be energetically advantageous. Although it is currently not logistically feasible to track flight speed and lipid content of individual insects through the course of a migration, multiple individuals sampled from within a migratory event can be used to test this hypothesis provided that the covariate of body size (and the associated positive allometry of flight speed; Dudley 2000) is also considered.

Many tropical migrant butterflies fly near the ground or vegetational canopies within their flight boundary layer such that insect airspeeds well exceed ambient winds (Johnson 1969; Srygley & Oliveira 2001). These flights typically occur over thousands of kilometres, and are characterized by extensive premigratory deposition of lipids as well as by nectaring *en route* (Williams 1930; Brown & Chippendale 1974; Walker 1980; Gibo & McCurdy 1993; Malcolm & Zalucki 1993). The optimization of energetic expenditure during flight is therefore likely to be important for successful long-range displacement in these taxa. However, no data are presently available on the airspeeds and relative lipid content of migratory butterflies. A migratory diurnal moth in the

*Correspondence author. E-mail: wings@berkeley.edu
†Current address. USDA-ARS-NPARL, 1500 North Central Avenue, Sidney, MT 59270, USA.

Neotropics, *Urania fulgens* (Walker), flies with substantial lipid reserves (12%–16% of total body mass) that are metabolized during flights of thousands of kilometres, but exhibits neither directional compensation for wind drift nor reduction in flight speed as endogenous lipids are depleted (Dudley & DeVries 1990; Srygley, Oliveira & Dudley 1996; Dudley *et al*. 2002).

Since 1991, we have been studying a multispecies system of migratory butterflies in the Republic of Panama. Although not exactly known, their migratory range is on the order of hundreds of kilometres from the Caribbean Sea to the Pacific coast of Panama. These butterflies are known to effect partial directional compensation for adverse winds together with a time-compensated sun compass (Srygley *et al*. 1996; Oliveira, Srygley & Dudley 1998; Srygley 2001a). Because of the more effective orientational system in these butterfly taxa relative to the moth *U. fulgens*, it is important to analyse possible lipid-associated variation in airspeed to determine if patterns of energetic expenditure during flight are similarly more sophisticated. Because airspeeds of multiple species can be measured directly in this particular migratory system (Dudley & Srygley 1994), no assumptions concerning magnitude or direction of simultaneous wind speed or direction are required. Study of these migrants thus permits direct evaluation of insect flight speed relative to lipid reserves.

Materials and methods

Field measurements of butterfly airspeeds during migrations were carried out from 1992 to 1997 over Lake Gatún in the vicinity of Barro Colorado Island. Using a small motorboat, we followed individual butterflies as they crossed the lake, matching their trajectory and speed in a parallel track over the water. Boat position was maintained such that the insect was anterior to and typically 2–3 m from one side of the boat. Under such conditions, an anemometer (VelociCalc Plus 1860; TSI Inc., Shoreview, MN, USA.) deployed laterally from the boat's prow and at the same height as the butterfly was used to measure speed of the boat relative to the surrounding air. This value was assumed to equal the butterfly's mean horizontal airspeed (DeVries & Dudley 1990; Dudley 1992); variable proximity of the boat yields equivalent airspeeds, ruling out active responses by the insect to the act of being followed. Escape behaviours include erratic flight and changes in course, which were observed after attempted captures. These are easily distinguishable from the natural migratory flight patterns characteristic of all the butterflies measured here. For 12 butterflies in 1997, a different method was used to obtain butterfly airspeeds (see Appendix in Srygley (2003) for calibration). Boat heading was measured with a flux-gate compass (Raytheon heading sensor M 92649; Raytheon, Waltham, MA, USA) mounted on the boat deck *c.* 0·5 m above the water line. Boat speed was measured with a transducer (Airmar P55/#20-039; Airmar, Milford, NH, USA) on a transom-mounted paddlewheel. Apparent wind direction and apparent wind speed were measured with a wind-vane and anemometer (KVH Quadro network speed/wind director; KVH Quadro, Middletown, RI, USA) mounted together on a 0·5-m aluminium pole that extended from the top of an L-shaped mast. The mast was attached to the boat to position the anemometer between 1·5 and 2 m above the water surface (i.e. at the height at which the butterflies flew) and in front of the boat to avoid wind

shear generated by the bow. Boat speed, its magnetic heading, the apparent wind speed and apparent wind heading were integrated with a KVH Quadro Concentrator (National Marine Electronics Association, Severna Park, MD, USA), from which wind speed and direction of the insect were calculated.

Following airspeed measurement, butterflies were then captured for subsequent morphological measurements, including wet body mass *m*, wing length *R* and the total wing area *S*, which includes the fore- and hindwings. Values of wing loading p_w (= m **g** S^{-1}, where **g** is gravitational acceleration) were also calculated for each butterfly. In 1992 and 1993, thoracic muscle temperatures of migrants were measured immediately following capture using standard thermocouple methods (see Srygley & Chai 1990). Wing condition was also categorized as fresh, intermediate or worn for all butterflies captured in 1992 and 1993. Because older butterflies may in general reallocate thoracic mass to reproductive structures (see Stjernholm *et al.* 2005), we used ancova with body mass as a covariate to assess possible variation in thoracic mass with both sex and wing wear (the latter as a proxy for age).

Lipid reserves used during migration were assumed to be located exclusively within the abdomen (Downer & Matthews 1976). Lipid contents were determined on butterflies using a standard 2 : 1 v/v chloroform : methanol extraction of the freeze-dried abdomen followed by measurement of the cuticular residue retained on quantitative filter paper (Folch, Lees & Stanley 1957; DeVries & Dudley 1990). Abdominal lipids were assumed to equal the difference in mass between the freeze-dried abdomen and the cuticular residue. This assumption may overestimate potential contributions of lipid reserves to flight metabolism, particularly for females with lipids dedicated within eggs, but represents an upper bound on available energetic substrate. We occasionally dissected female butterflies to assess the number of mature eggs. Lean body mass was estimated as the initial wet body mass minus the calculated abdominal lipid mass.

Standard linear regressions of log-transformed data were used to assess the morphological and allometric correlates of intraspecific variation in flight speed. We also regressed residuals from regressions of airspeed on lean body mass against residuals from regressions of lipid mass on lean body mass to control for overall size-related correlates of flight speed. Finally, we calculated partial correlation coefficients among flight speed, body mass and lipid mass to test among individuals the effect of variable lipid mass at constant body mass, and *vice versa*, on flight speed. A *t*-test was used to determine the statistical significance of each partial correlation coefficient (Zar 1984).
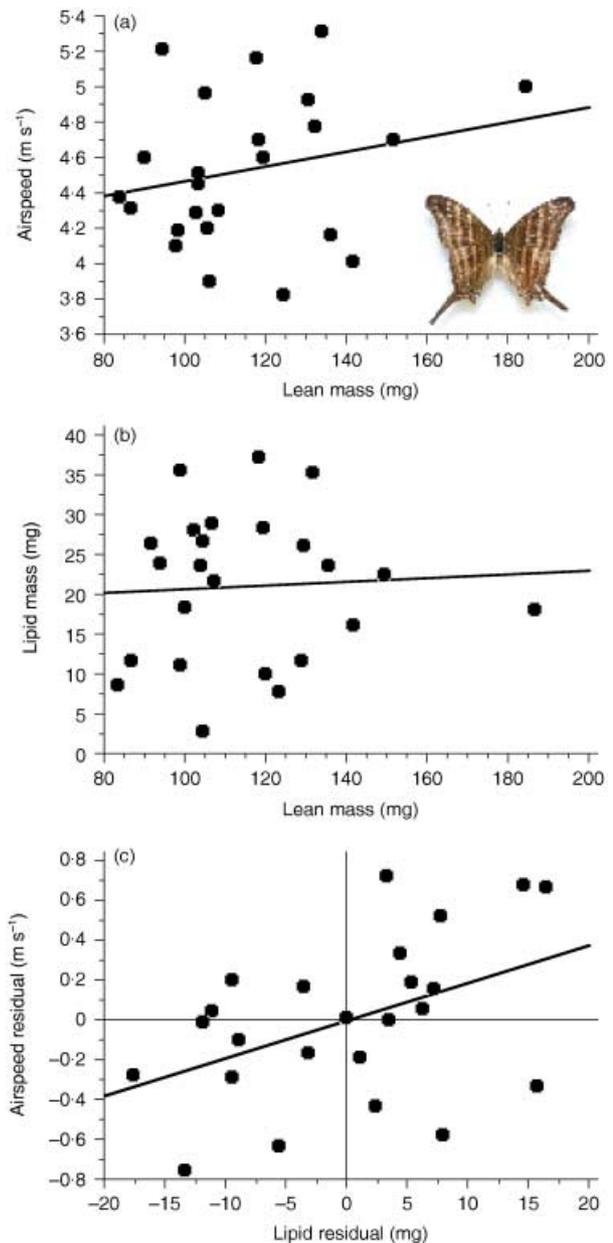
Results

Flight speeds, abdominal lipid content and morphological data were obtained for 10 species of migratory butterflies. Airspeeds during migration for these species ranged from about 3 to 7 m s^{-1}, and averaged about 4·9 m s^{-1} for the 10 study species (Table 1; Figs 1a and 2a). Relative abdominal lipid mass averaged 9·4%, ranging among species from 4·5% to 15·6% of body mass (Table 1; Figs 1b and 2b). Application of two-way anova revealed significant differences in morphology and airspeeds both among species and between genders (Table 2). Species differed significantly in all morphological parameters investigated, whereas gender differences were significant only in body mass (two of the species × gender interactions were also significant). Five of the investigated species (*Aphrissa boisduvalii* Felder, *A. statira*
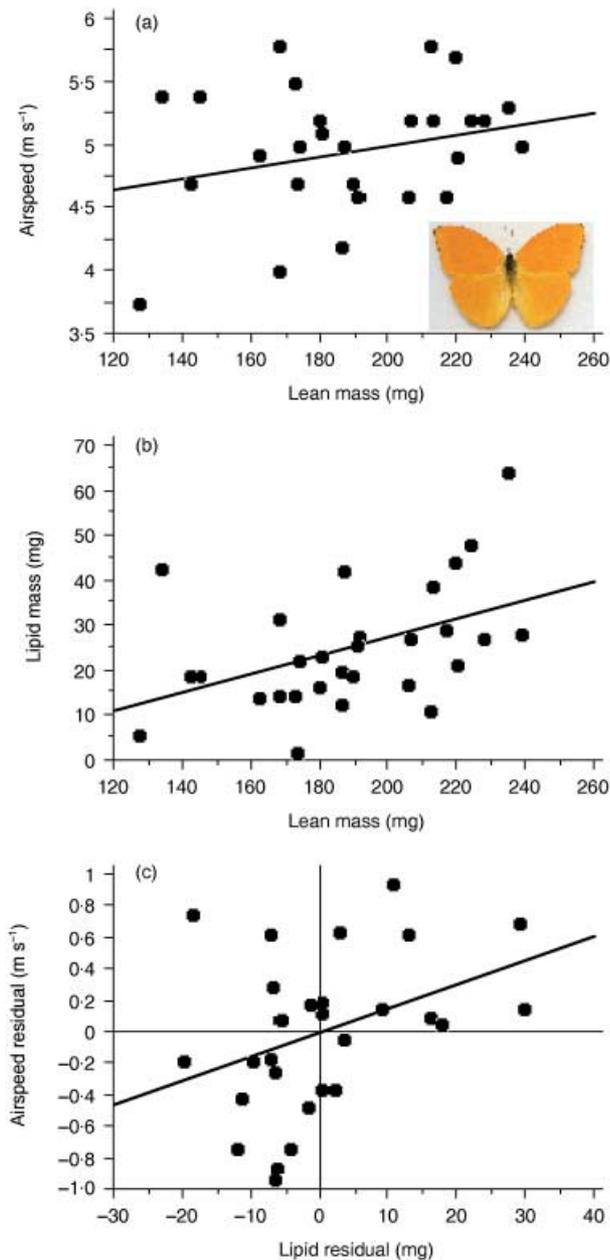
Fig. 1. (a) Relationship between airspeed and lean body mass for migrating *Phoebis argante* males. The regression is given by: $y = 4\cdot12 + 0\cdot004x$, $R^2 = 0\cdot07$, NS. The inset illustrates a male *P. argante*. (b) Relationship between lipid mass and lean body mass for the same individuals. The regression is given by: $y = -13\cdot5 + 0\cdot21x$, $R^2 = 0\cdot20$, $P < 0\cdot02$. (c) Relationship between residuals of airspeed regressed on lean body mass (a) and residuals of lipid mass regressed on lean body mass (b). The regression is given by: $y = 0\cdot015x$, $R^2 = 0\cdot14$, $P < 0\cdot05$.

Fig. 2. (a) Relationship between airspeed and lean body mass for migrating *Marpesia chiron* females. The regression is given by: $y = 4\cdot04 + 0\cdot004x$, $R^2 = 0\cdot05$, NS. The inset illustrates a female *M. chiron*. (b) Relationship between lipid mass and lean body mass for the same individuals. The regression is given by: $y = 18\cdot5 + 0\cdot023x$, $R^2 = 0\cdot0003$, NS. (c) Relationship between residuals of airspeed regressed on lean body mass (a) and residuals of airspeed regressed on lipid mass (b). The regression is given by: $y = 0\cdot019x$, $R^2 = 0\cdot19$, $P < 0\cdot04$.

Cramer, *Marpesia chiron* Fabricius, *M. petreus* Cramer and *Phoebis argante* Fabricius; see Table 1) had sample sizes exceeding 14 for one of the two genders, and these data subsets were then used for focal analysis of airspeeds in relation to lipid reserves and other morphological variables. Within each of these species/gender subsets, one-way ANOVA was used to assess among-year variation in airspeed and in the morphological variables given in Table 1. With only one

exception (the wing length of female *A. boisduvalii*), all morphological variables as well as airspeed were independent of study year ($P > 0\cdot05$ following sequential Bonferroni correction; Holm 1979). Data within each of these species/gender subsets were accordingly pooled by year for analysis of relationships between airspeed and morphological variables.

Within each of the five aforementioned species/gender subsets, linear regressions of log-transformed airspeed on

Table 1. Mean airspeed and morphological parameters (with standard deviations) for 10 migratory species with genders and sample sizes

Species	Sex (n)	Wet body mass (mg)	Relative lipid mass (% wet body mass)	Wing length (mm)	Wing loading (N m^{-2})	Airspeed (m s^{-1})
Aphrissa boisduvalii	Male (5)	187·2 (56·1)	7·9 (1·7)	33·1 (1·0)	1·06 (0·18)	4·8 (0·7)
	Female (14)	201·1 (29·9)	12·4 (4·0)	33·6 (1·4)	1·07 (0·16)	5·0 (0·5)
Aphrissa statira	Male (16)	199·8 (36·9)	10·3 (4·2)	33·1 (1·6)	1·14 (0·20)	5·2 (0·5)
	Female (7)	179·9 (31·9)	10·0 (4·8)	32·7 (1·5)	1·12 (0·10)	4·6 (0·7)
Appias drusilla	Male (3)	129·3 (43·6)	4·8 (2·0)	34·7 (0·8)	0·77 (0·14)	4·3 (0·8)
	Female (3)	135·9 (26·3)	5·9 (1·9)	32·8 (1·6)	0·78 (0·13)	4·5 (1·2)
Historis acheronta	Male (5)	543·2 (108·9)	9·6 (3·6)	43·7 (3·2)	2·24 (0·30)	6·6 (0·5)
	Female (4)	480·3 (174·9)	10·6 (7·1)	39·0 (4·1)	2·30 (0·58)	6·5 (0·5)
Marpesia chiron	Male (6)	106·4 (20·3)	8·7 (5·9)	30·3 (1·4)	0·81 (0·14)	3·7 (1·0)
	Female (24)	135·7 (25·4)	15·4 (6·4)	31·3 (1·0)	1·07 (0·24)	4·5 (0·4)
Marpesia petreus†	Male (1)	195·9 (33·7)	15·6 (10·6)	39·3 (2·7)	1·08 (0·18)	4·6 (0·6)
	Female (18)					
Phoebis argante	Male (29)	213·8 (38·1)	11·5 (5·1)	36·3 (1·8)	0·93 (0·11)	4·9 (0·5)
	Female (6)	251·8 (17·2)	7·8 (1·8)	37·0 (1·3)	1·06 (0·13)	4·6 (0·5)
Phoebis philea†	Male (1)	482·8 (104·6)	7·5 (1·1)	44·0 (1·8)	1·39 (0·18)	5·0 (0·5)
	Female (3)					
Phoebis sennae†	Male (2)	262·9 (156·4)	8·1 (1·7)	38·0 (5·8)	1·11 (0·32)	4·7 (0·7)
	Female (4)					
Phoebis trite†	Male (1)	185·4 (34·8)	4·5 (2·4)	33·6 (0·6)	0·84 (NA)‡	4·4 (0·1)
	Female (1)					

†Genders pooled because of low sample size for either one or both sexes.
‡The standard deviation was not calculated because the datum for one individual was missing.

Table 2. *F*-statistics from two-way ANOVA's for the effects of species, gender and their interaction on variation in each of five morphological parameters or airspeed

Dependent variable	Species (9, 129)	Gender (1, 129)	Species × Gender (9, 129)
Wet body mass	60·2*	10·4*	4·3*
Lipid mass	5·0*	3·4	1·6
Wing length	40·1*	2·3	4·7*
Airspeed	12·9*	1·2	2·4
	Species (6, 115)	Gender (1, 115)	Species × Gender (6, 115)
Wing area†	36·5*	1·5	1·0
Wing loading†	56·2*	4·4	1·0

Degrees of freedom are in parentheses.
*$P < 0.05$ following sequential Bonferroni adjustment.
†*Phoebis philea*, *P. sennae* and *P. trite* were excluded because of low sample sizes.

log-transformed values of body mass, lipid mass, wing length, wing area and wing loading revealed only one significant correlation following sequential Bonferroni correction from an initial α-level of $P = 0.05$. Following log-transformation, airspeed was positively correlated with wing loading for female *M. chiron* ($R^2 = 0.29$; $P < 0.001$), but none of the other log–log regressions were significant. Within-species variation in airspeed relative to individual morphological variables was therefore of little significance, primarily because of tight correlations among the morphological variables and the low overall range of airspeeds for any given species (coefficients of variation typically 10%–25%; see Table 1). However, linear

regressions between residuals of airspeed regressed on lean body mass and residuals of lipid mass regressed on lean body mass were significantly positive for the five species/gender subsets ($P < 0.05$ in all cases; Figs 1c and 2c). These results indicate that, as predicted, those individual butterflies that flew at higher airspeeds with respect to the size-controlled average also exhibited relatively greater values for abdominal lipid content.

Partial correlations between airspeed, wet body mass and lipid mass were determined to assess indirectly the hypothesis that depletion of lipid reserves is associated with a decline in airspeed among different individuals of varying total body mass. For three of the five data subsets, airspeed was positively correlated with wet body mass when lipid mass was held constant (Table 3), indicating that larger butterflies in these groups flew faster, independent of abdominal lipid content. Similarly, airspeed was positively correlated with lipid mass when wet body mass was held constant in four of the five data subsets (see Table 3). For one data subset (*A. boisduvalii* females), this correlation was negative but non-significant using a two-sided test ($P < 0.10$), but was significantly negative using a one-sided test ($P < 0.05$); this subset also had the lowest sample size ($N = 14$). Because each of the five species/gender subsets represents an independent test of the hypothesis that airspeeds should decline as lipid reserves are depleted, Fisher's combination of significance test (Sokal & Rohlf 1995) was used to assess the overall significance of the five partial correlations. This test revealed a strong positive effect of wet body mass on airspeed when lipid mass was held constant ($\chi^2 = 35.5$, 10 d.f., $P < 0.001$), and an even stronger positive effect of lipid mass on airspeed when wet body mass was held constant ($\chi^2 = 55.3$, 10 d.f., $P < 0.001$).

Table 3. Partial correlation coefficients relating butterfly airspeed to either wet body mass or abdominal lipid mass for five species/gender data subsets

Data subset	n	Wet body mass	Abdominal lipid mass
Aphrissa boisduvalii females	14	0·273 (*t*-stat = 0·466, *P* < 0·001)	–0·155 (*t*-stat = 1·692, *P* < 0·10)
Aphrissa statira males	16	–0·164 (*t*-stat = 0·941, *P* < 0·02)	0·424 (*t*-stat = 0·375, *P* < 0·001)
Marpesia chiron females	24	0·232 (*t*-stat = 1·093, *P* < 0·001)	0·331 (*t*-stat = 1·607, *P* < 0·001)
Marpesia petreus females	18	–0·235 (*t*-stat = 0·936, *P* < 0·001)	0·430 (*t*-stat = 1·845, *P* < 0·001)
Phoebis argante males	29	0·091 (*t*-stat = 0·576, *P* < 0·02)	0·315 (*t*-stat = 1·622, *P* < 0·001)

For all butterflies captured in 1992 and 1993, thoracic temperatures during migration ranged between 34 °C and 41 °C. Flight speed was positively correlated with thoracic temperature for female *M. petreus* ($P < 0.05$), but not for any of the other gender/species subsets under consideration ($P > 0.25$ in each case). Behaviourally, all migrants were observed to be primarily active during mid-day hours (09.00–15.00 h) when both solar radiation and ambient air temperature were high, suggesting a restricted range of muscle temperatures preferred for flight (see Srygley & Chai 1990).

Except for *M. chiron*, thoracic mass showed no statistical association with wing wear using wet body mass as a covariate ($P > 0.05$ in all cases). In *M. chiron*, body mass-adjusted thoracic mass did not differ significantly between males and females, and using pooled data from the two sexes showed significant reductions with both body mass and wing wear (ANCOVA, $F = 16.2$, d.f. = 2,7, $P = 0.002$; body mass, $P = 0.035$; wing wear, $P = 0.051$).

Discussion

Airspeeds of migrating butterflies ranged from about 4 to nearly 7 m s^{-1}, and demonstrated considerable variation among species that undoubtedly derives from significant differences among the study taxa in wet body mass and in wing loading (Tables 1 and 2). Lipid content was similarly variable, ranging from about 4% to 16% of total body mass. Relative lipid masses tended to be somewhat lower than mean values (12%–16%) reported for the diurnal moth *U. fulgens* that migrates through central Panama at the same time of year (DeVries & Dudley 1990; Dudley *et al.* 2002). Within each of the five gender/species subsets for which sufficient data were available, results from both regressions of airspeed residuals and partial correlations demonstrated a positive correlation between flight speed and relative lipid reserves in migratory butterflies, consistent with optimization of maximum range speed. Although it was not possible to measure relevant mass and speed variation in individual butterflies, data from multiple individuals clearly show significant correlations between flight speed and abdominal lipid content when covariance in body size is taken into account (Fig. 1; Table 3).

This trend thus conforms qualitatively to the predictions of Pennycuick (1969), which presuppose a 'U'-shaped power curve relating the metabolic costs of flight to forward airspeed. For such a power curve, metabolic expenditure is least at some intermediate flight speed relative to either lower flight speeds, or more markedly, at higher flight speeds. Power curves have not been constructed for the butterflies considered here, although a sharply 'U'-shaped curve is likely for the migratory moth *U. fulgens* that flies with comparable airspeeds and wingbeat kinematics (Dudley & DeVries 1990; Dudley 2000). The high advance ratios in *U. fulgens* (i.e. the ratio of forward speed to the mean flapping speed of the wings) also likely characterize the flight of migratory butterflies, suggesting that changes in forward airspeed will have pronounced effects on wing aerodynamics and total power expenditure during flight (Dudley 2000). Choice of flight speed can thus strongly influence the rate of energetic expenditure, and is therefore likely to be an important target of selection for long-distance migrants. However, optimal flight speeds may also depend on the amount of time spent accumulating energy reserves prior to migration, as well as on rates of energetic uptake during migration (Alerstam & Lindström 1990; Hedenström & Alerstam 1995). This latter possibility has the net effect of reducing net costs of flight per unit time if uptake is continuous across the migratory range. The butterfly species have been observed to nectar during the course of migration (R. B. Srygley and R. Dudley, personal observations), although the net rate of energy intake relative to expenditure during flight is unknown. Relative lipid mass may also influence the risk of predation and subsequent evasion. Nonetheless, flight speed adjustment in response to changing energetic reserves and total body mass is potentially an important cost-saving strategy.

Additional evidence that these migratory butterflies assess their internal energetic state comes from a study over the Caribbean Sea (Srygley 2001a, 2001b), near the easterly origin of the migratory flyways of some of the species considered here. As they departed the Colombian coast near Cartagena, migrating *P. sennae* butterflies flew westerly in the morning apparently to intercept offshore trade winds and to continue to the coast of Central America. However, they slowly altered their orientation towards the southeast as the day proceeded, a direction which would bring them back to the Colombian coast for refuge and nectaring. Females altered their courses earlier in the day than did males, and also reduced airspeed in tailwinds consistent with maximization of migratory range, whereas males did not (Srygley 2001b). It is possible that female butterflies are more sensitive than males relative to energetic state during migration because of lipid requirements for egg production.

Here, we did not decouple egg from total abdominal lipid contributions in females, but up to 50% of captured female butterfly migrants exhibited mature ovarioles. This proportion was however highly variable among species. Similarly, variation in egg number among individual females of the same species was high; for example, the number of mature eggs in those *A. statira* females with mature ovarioles ranged from 0 to more than 30. We found that both male and female butterflies exhibited similar trends in airspeed adjustment relative to lipid mass (e.g. Table 3). Thus, although reproductive maturity is likely to play a role in an individual's assessment of lipid reserves, it has not obscured the general pattern of a reduction in airspeed with lipid reserves as predicted from aerodynamic theory.

Age-related reallocation of mass from the thorax to the abdomen (Karlsson 1994; Stjernholm *et al.* 2005) was not possible to assess systematically, because older wing-worn migrants are rare to non-existent. Only in *M. chiron* did wing wear tend to be correlated with variation in body mass parameters. Future assessment of both gender- and age-based variation in flight speed and lipid allocation would be best confined to the more numerous migrants (e.g. *A. statira*) for which one might occasionally find older adults.

The nymphalid and pierid butterfly taxa studied here are taxonomically diverse, and migratory butterflies in general may adjust airspeed for changes in lipid mass in a manner consistent with maximizing their migratory range. Similarly, monarch butterflies (*Danaus plexippus*) are capable of navigating to specific destinations and likely compensate for crosswind drift (Schmidt-Koenig 1985). In favourable tailwinds, monarch butterflies also soar at higher altitudes which reduces the energetic cost of flight (Gibo & Pallett 1979) but increases the flight time to destination (Garland & Davis 2002). All migratory butterflies fly during the day typically near to the surface of the earth, and likely use optic flow to gauge their speed and drift (Srygley 2001a). In contrast to the compensatory results demonstrated here for butterflies, however, airspeeds of migrating *U. fulgens* moths are independent of both body mass and abdominal lipid mass (Dudley *et al.* 2002). This diurnal moth species is also unable to adjust its course direction to compensate for wind drift (Srygley *et al.* 1996), although its migratory range is comparable to those of the butterflies studied here, and it similarly visits flowers during migration (R. B. Srygley and R. Dudley, personal observations). Although there are no other studies of optimal migratory behaviours in migratory butterflies and moths, *U. fulgens* (Uraniidae) belongs to a lineage basal to the butterflies (Papilionoidea). Differences between the butterflies studied here and *U. fulgens* in the abilities to adjust airspeed for lipid content, and to compensate for crosswind drift over water, reflect the origin of sophisticated control and guidance systems pertaining to migration at least once within the Papilionoidea.

Acknowledgements

References

Alerstam, T. & Lindström, Å. (1990) Optimal bird migration: the relative importance of time, energy, and safety. *Bird Migration* (ed. E. Gwinner), pp. 331–351. Springer-Verlag, Berlin.

Brown, J.J. & Chippendale, G.M. (1974) Migration of the monarch butterfly *Danaus plexippus*: energy sources. *Journal of Insect Physiology*, **20**, 1117–1130.

DeVries, P.J. & Dudley, R. (1990) Morphometrics, airspeeds, thermoregulation and lipid reserves of migrating *Urania fulgens* (Uraniidae) moths in natural free flight. *Physiological Zoology*, **63**, 235–251.

Downer, R.G.H. & Matthews, J.R. (1976) Patterns of lipid distribution and utilisation in insects. *American Zoologist*, **16**, 733–745.

Dudley, R. (1992) Aerodynamics of flight. *Biomechanics (Structures & Systems): A Practical Approach* (ed. A.A. Biewener), pp. 97–121. Oxford University Press, Oxford.

Dudley, R. (2000) *The Biomechanics of Insect Flight: Form, Function, Evolution*. Princeton University Press, Princeton, NJ.

Dudley, R. & DeVries, P.J. (1990) Flight physiology of migrating *Urania fulgens* (Uraniidae) moths: kinematics and aerodynamics of natural free flight. *Journal of Comparative Physiology A*, **167**, 145–154.

Dudley, R. & Srygley, R.B. (1994) Flight physiology of Neotropical butterflies: allometry of airspeeds during natural free flight. *The Journal of Experimental Biology*, **191**, 125–139.

Dudley, R., Srygley, R.B., Oliveira, E.G. & DeVries, P.J. (2002) Flight speeds, lipid reserves, and predation of the migratory moth *Urania fulgens* (Uraniidae). *Biotropica*, **34**, 120–126.

Folch, J., Lees, M. & Stanley, G.H. (1957) A simple method for the isolation and purification of total lipides from animal tissues. *The Journal of Biological Chemistry*, **226**, 497–509.

Garland, M.S. & Davis, A.K. (2002) An examination of Monarch butterfly (*Danaus plexippus*) autumn migration in coastal Virginia. *The American Midland Naturalist*, **147**, 170–174.

Gibo, D.L. & Mccurdy, J.A. (1993) Lipid accumulation by migrating monarch butterflies (*Danaus plexippus* L.). *Canadian Journal of Zoology*, **1**, 76–82.

Gibo, D.L. & Pallett, M.J. (1979) Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. *Canadian Journal of Zoology*, **57**, 1393–1401.

Green, M. & Alterstam, T. (2000) Flight speeds and climb rates of Brent geese: mass-dependent differences between spring and autumn migration. *Journal of Avian Biology*, **31**, 215–225.

Hedenström, A. & Alerstam, T. (1995) Optimal flight speed of birds. *Philosophical Transactions of the Royal Society of London. Series B*, **348**, 471–487.

Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Johnson, C.G. (1969) *Migration and Dispersal of Insects by Flight*. Methuen & Co Ltd, London.

Karlsson, B. (1994) Feeding habits and change of body composition with age in three nymphalid butterfly species. *Oikos*, **69**, 224–230.

Malcolm, S.B. & Zalucki, M.P.E. (1993) *Biology and Conservation of the Monarch Butterfly*. Natural History Museum of Los Angeles County, Los Angeles.

Oliveira, E.G., Srygley, R.B. & Dudley, R. (1998) Do Neotropical migrant butterflies navigate using a solar compass? *The Journal of Experimental Biology*, **201**, 3317–3331.

Pennycuick, C.J. (1969) The mechanics of bird migration. *Ibis*, **111**, 525–556.

Pennycuick, C.J. (1978) Fifteen testable predictions about bird flight. *Oikos*, **30**, 165–176.

Schmidt-Koenig, K. (1985) Migration strategies of monarch butterflies. *Migration: Mechanisms and Adaptive Significance* (ed. M.A. Rankin), pp. 786–798. Marine Science Institute, Port Aransas, TX.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman, New York, NY.

Srygley, R.B. (2001a) Compensation for fluctuations in crosswind drift without stationary landmarks in butterflies migrating over seas. *Animal Behaviour*, **61**, 191–203.

Srygley, R.B. (2001b) Sexual differences in tailwind drift compensation in *Phoebis sennae* butterflies (Lepidoptera: Pieridae) migrating over sea. *Behavioral Ecology*, **12**, 607–611.

Srygley, R.B. (2003) Wind drift compensation in migrating dragonflies *Pantala* (Odonata: Libellulidae). *Journal of Insect Behaviour*, **16**, 217–232.

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

Srygley, R.B. & Oliveira, E.G. (2001) Orientation mechanisms and migration strategies within the flight boundary layer. *Insect Movement: Mechanisms and Consequences* (eds I.P. Woiwod, D.R. Reynolds & C.D. Thomas), pp. 183–206. CAB International, Oxford.

Srygley, R.B., Oliveira, E.G. & Dudley, R. (1996) Wind drift compensation, flyways, and conservation of diurnal, migrant Neotropical Lepidoptera. *Proceedings of the Royal Society of London*, **263**, 1351–1357.

Stjernholm, F., Karlsson, B. & Boggs, C.L. (2005) Age-related changes in thoraicic mass: possible reallocation of resources to reproduction in butterflies. *Biological Journal of the Linnean Society*, **86**, 363–380.

Walker, T.J. (1980) Migrating Lepidoptera: are butterflies better than moths? *Florida Entomologist*, **63**, 79–98.

Williams, C.B. (1930) *The Migration of Butterflies*. Oliver and Tweed, London.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs, NJ.