Flight Speeds, Lipid Reserves, and Predation of the Migratory Neotropical Moth *Urania fulgens* (Uraniidae)[1]

ABSTRACT

Aerodynamic theory predicts that migrant fliers should reduce their speed of flight as endogenous energy reserves are gradually consumed. This prediction was tested for *Urania fulgens* (Walker) moths migrating through central Panama in 1987 and again in 1998. Direct airspeed measurements together with chloroform:methanol extractions of abdominal lipids were used to determine that, contrary to theoretical predictions, the speed of flight among individuals was independent of both body mass and abdominal lipid mass.

Key words: airspeed; flight; lipids; migration; Panama; predation; Urania fulgens.

LONG-DISTANCE MIGRATION BY FLIGHT entails considerable energetic expenditure. To meet such demands, insect and avian migrants typically engage in premigratory lipid loading that substantially increases total body mass (Johnson 1968, Alerstam 1990). As these energy reserves are gradually consumed through the course of a migration, total body mass declines and concomitantly results in a decrease in the total cost of flight. Migrants may then adjust their flight speeds so as to maintain a constant and optimally low ratio of energetic expenditure relative to their translational speed. In particular, flight speed is predicted to vary with the square root of body mass if individuals are maximizing the distance traveled per unit energy expended (Pennycuick 1978). Although this prediction refers to reduction in airspeed as individuals consume endogenous reserves, logistical difficulties generally preclude evaluation of this hypothesis for any given migrant flying over long distances. Instead, comparisons of different individuals sampled from within a migratory event can be used to determine if those migrants with smaller body masses and reduced lipid reserves are also slower fliers. Because insect flight speeds tend to scale positively with body mass (Dudley 2000), large sample sizes are, however, necessary to decouple statistically the effects of lipid depletion from overall body size variation.

Butterflies and moths migrating within their flight boundary layer (*sensu* Taylor 1958) represent an interesting case with which to test this prediction. Premigratory lipid loading is characteristic of most if not all lepidopteran migrants, as exemplified by the extensive fat reserves accumulated by monarch butterflies prior to autumnal flight (Brown & Chippendale 1974, Gibo & McCurdy 1993). Migratory butterflies and diurnal moths may fly for thousands of kilometers (Williams 1930, Malcolm & Zalucki 1993), and minimization of energy costs is likely to be critical for successful migration. Also, such boundary layer migrants often obtain nectar along the course of their flight route, and this energy uptake is likely necessary for successful long-range displacement (Walker 1980, Dudley & DeVries 1990). In contrast to the substantial data available on the energy balance of migrating birds (Alerstam 1990, Berthold 1993), virtually no relevant airspeed and lipid data are available for migrating insects. The ecological impact of predation along the course of a migratory pathway may also be of significance for insects within the flight boundary layer. Butterflies and moths may be particularly vulnerable to predators when nectaring at flowers, but quantitative features of predation have never been assessed for migratory representatives of these taxa.

The diurnal uraniid moth *Urania fulgens* undertakes often spectacular long-distance migrations in Central and South America (Williams 1930; Skutch 1970; Young 1970; Smith 1972, 1983, 1992). Previous work on these migrants has evaluated the energetic costs of flight (DeVries & Dudley 1990, Dudley & DeVries 1990) as well as their apparent inability to compensate for directional drift when confronted by adverse winds (Srygley *et al.* 1996). The migratory range of this species may be as great as several thousand kilometers, and at least some flight may occur over open water across the southern reaches of the Caribbean Sea (Srygley, pers. obs.). As part of ongoing investigations into the ecophysiology of Neotropical lepidopteran migrations, we measured airspeeds, various parameters of wing and body

TABLE 1.   *Study year, gender, mean body mass (range), mean airspeed (range), and mean relative lipid content (range) of migrating* Urania fulgens *moths. Unless otherwise indicated, data refer to moths undamaged by predators. Damaged individuals in 1998 were all female.*

Year	Gender	Body mass (g)	Mean airspeed (m/sec)	Relative lipid content (% body mass)
1987	F ($N = 13$)	0.401 (0.265–0.599)	3.7 (2.4–6.0)	12.1 (5.3–19.1)
1998	F ($N = 37$)	0.522 (0.255–0.839)	3.9 (3.0–4.7)	16.0 (4.0–27.0)
1987	M ($N = 12$)	0.278 (0.222–0.328)	4.1 (2.9–5.3)	12.0 (7.0–21.5)
1998	M ($N = 7$)	0.347 (0.314–0.407)	3.6 (2.7–4.1)	13.5 (5.8–23.7)
1998 (damaged)	F ($N = 17$)	0.526[a] (0.295–0.755)	3.7[a] (2.7–4.8)	28.1[b] (18.2–38.3)

[a] Statistically indistinguishable from the corresponding value for undamaged 1998 females (one-way ANOVA, $P > 0.05$).
[b] Both absolute and relative lipid mass significantly different than that of undamaged 1998 females (one-way ANOVA, $P < 0.0001$ in both cases).

morphology pertaining to size, and lipid content of *U. fulgens* during major migrations of 1987 and 1998. Although *U. fulgens* migrates annually through central Panama, migratory intensity is highly variable in space and time (Smith 1992). The predictive ability necessary to obtain measurements from large sample sizes under field conditions is accordingly limited. Here we report results from two particular migrations during which it was possible to observe and capture large numbers of individual moths, as well as to make incidental observations of predator-induced damage and actual predation events.

Migrating *U. fulgens* were studied in October 1987 and again in October 1998 in the vicinity of Barro Colorado Island, Lake Gatún, Republic of Panama. Individual moths flying over the lake's surface were followed in a motorboat such that the trajectories of the moth and of the boat were nominally parallel and of equivalent speed. A unidirectional anemometer (1987: TSI Model 1650; 1998: Velocicalc Plus 1860) deployed laterally from the prow of the boat was used to measure the speed of the boat relative to the surrounding air; this value was presumed to equal the airspeed of the flying moth (DeVries & Dudley 1990, Dudley 1992). From one to three separate measurements of airspeed (average: 1.55) were made on each moth; the insect was then captured and kept within a glassine envelope for subsequent morphological measurements within three hours of capture. In 1998, measurements of wind speed, wind direction, and the track direction of each moth (*i.e.,* the compass direction of flight) were also obtained immediately following capture. These measurements of track direction were probably accurate only to one-eighth of a compass point (*i.e.,* to within *ca* 6º), although no systematic orientational bias would have been introduced by this method.

Morphological measurements taken on each moth included the wet body mass *m,* the wing length *R,* and the total wing area *S* (calculated by doubling the value for one wing pair obtained using a flatbed scanner, with the fore- and hindwings overlapped approximately as in flight). Values of wing loading p_w (= mg/S, where g is gravitational acceleration) were calculated for each insect. Lipid reserves used during migration were assumed to be located exclusively within the abdomen (Downer & Matthews 1976), which was first freeze-dried for 24 hours and then weighed. Total lipids were extracted from the dried abdomen with a chloroform/methanol solution (2:1 v/v) following the method of Folch *et al.* (1957). The mass of the remaining non-lipid constituents (primarily cuticle) was determined to the nearest mg, and was subtracted from the initial dry abdominal mass to yield the dry mass of lipids presumed to be available to fuel flight. This approach may falsely attribute non-lipid constituents extracted in chloroform: methanol (*e.g.*, alkaloids) to estimates of lipid mass, but we here assume that such compounds are present in insignificant quantities relative to stored abdominal lipids. Particularly for female moths with lipids potentially dedicated within eggs, this estimate of available lipids may also overestimate the potential contributions of endogenous reserves to flight metabolism, but is presented here as an upper bound on available energetic substrate. During both study periods, opportunistic observations were also made of predation by birds on migrating moths.

Airspeeds of undamaged *U. fulgens* moths during migration ranged from 2.4 to 6.0 m/sec ($\bar{x}$ = 3.9 m/sec; Table 1). Abdominal lipid contents were similarly variable, ranging from 4.0 to 38.3 percent of

total body mass ($\bar{x}$ = 13.9%; Table 1). Two-way ANOVA with year and gender as factors (df = 1, 65) showed, following sequential Bonferroni adjustment (Holm 1979), significant effects of both factors on body mass (year effect: F = 9.0, P < 0.001; gender effect: F = 22.6, P < 0.001; year × gender effect, F = 0.4, NS) and on lipid mass (year effect: F = 4.2, P < 0.01; gender effect: F = 6.5, P < 0.01; year × gender effect, F = 0.7, NS). Females tended to have higher body and lipid masses, whereas moths captured in 1987 were less heavy and contained less lipid than those captured in 1998 (Table 1). Two-way ANCOVA using year and gender as factors showed no significant effect of either factor on the relationship between airspeed and body mass, or on the relationship between airspeed and lipid mass (P > 0.05 in both cases). Of 11 higher order interactions among variables in this ANCOVA, one third-level (year × gender × lipid) and one fourth-level interaction (year × gender × lipid × mass) were significant (0.02 < P < 0.05 in each case). Because of these significant higher order interactions, separate analyses for each of the four year × gender subsets were carried out.

Possible effects of body size on airspeed in undamaged moths were considered by analyzing correlations between log-transformed airspeed and log-transformed size variables (*i.e.,* body mass, dry lipid mass, wing length, and wing loading) for each of the year × gender subgroups (1987/1998 × male/female). All such correlations were nonsignificant at P > 0.05. The hypothesis that airspeed declines as an individual migrating moth depletes its lipid reserves can also be indirectly tested using data for different individuals by evaluating the partial correlation between airspeed and lipid mass while simultaneously controlling for the effects of variable body mass. The statistical significance of partial correlation coefficients can then be tested using a *t*-test (Zar 1984). None of the four year × gender subsets showed significant partial correlations between airspeed and lipid mass (*t*-test, P > 0.05 in all cases); nor were such partial correlations significant for either male or female *U. fulgens* pooled from each of the two study years (*t*-test, P > 0.05 in both cases).

For moths captured in 1998, values for the wind speed, wind direction, and each moth's track direction were used to calculate the head-/tailwind component to the moth's ground speed (Srygley *et al.* 1996). Airspeed was then regressed against the head-/tailwind component to assess possible behavioral compensation for adverse or advantageous winds. Neither female nor male *U. fulgens* demonstrated a significant relationship between airspeed and the head-/tailwind component of ambient winds (females: N = 33, R^2 = 0.007, P = 0.64; males: N = 7, R^2 = 0.10, P = 0.49). Mean track direction (± 95% confidence limits) in 1998 was 10 ± 12° (Hodges–Ajne test: N = 63, r = 47, a = 0.746).

Airspeeds, body masses, wing lengths, and wing loadings of damaged female moths captured in 1998 were comparable to those of undamaged females (one-way ANOVA, P > 0.05 in all cases); abdominal lipid mass of damaged individuals was, however, approximately twice that of undamaged moths (one-way ANOVA, P < 0.001; Table 1). Two specific observations confirmed predation on migratory *U. fulgens* in central Panama. On 7 October 1987, when migrant numbers were considerable, a large number of *U. fulgens* was seen floating in the water off Barbour Point, Barro Colorado Island. Fourteen of these moths (13 females/1 male) were recovered, all of which were found to have wing and/or body damage, including beak marks on the wings, missing fore- or hindwings, and torn or missing abdomina. During the several hours prior to recovery of these damaged individuals, Mangrove Swallows (*Tachycineta albilinea*) were observed attacking the migrating moths in flight over the lake. On 19 June 1995, an individual *U. fulgens* was spotted floating in the water north of Barro Colorado Island. This insect flew off upon approach, but was subsequently captured once it landed in the water. Upon inspection, the moth was found to be missing its abdomen and to have damaged hindwings. As with the majority of those damaged moths captured in 1998, substantial damage to the wings and/or body did not preclude flight in the prevailing migratory direction by this individual.

Airspeeds of migrating *U. fulgens* moths were found to be independent of both body mass and lipid mass. Similarly, partial correlations between airspeed and lipid mass that incorporated effects of covarying body mass were also nonsignificant. These results suggest that individual moths do not adjust flight speeds as lipid reserves are gradually depleted, and are thus not optimizing their maximum migratory range. Instead, *U. fulgens* may try to minimize the total time spent traveling, or may adopt a mixed strategy varying with energetic rewards provided by the landscape mosaic (including anthropogenic perturbations) over which they fly. Optimal flight speeds in this case will 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 incremental uptake is continuous across the migratory range. It is likely that *U. fulgens* engages in en route nectaring to acquire energy for flight, as the postulated migratory distances for this species are well in excess of those attainable using typical amounts of endogenous reserves (Dudley & DeVries 1990). Nectaring by *U. fulgens* on *Inga* (Leguminosae) flowers has been observed in the field (Smith 1982), although the relative proportion of migratory time spent obtaining additional fuel is not known. The analytical situation is further complicated by possible energy uptake during stopovers, whereby such factors as rate of lipid deposition and vulnerability to predation influence predictions of optimal flight speed (Lindström & Alerstam 1992; Weber *et al.* 1994, 1998). Finally, moths flying over Lake Gatún may also alter behavior relative to their much more representative long-distance flight over varied and complex landscapes; this possibility cannot be assessed without substantially more data on natural flight performance.

Inherent to the predictions of Pennycuick (1978) is the assumption of a "U"-shaped power curve relating the energetic costs of flight to forward airspeed. For *U. fulgens*, kinematic and biomechanical data obtained on different individuals suggest a minimum expenditure near 1.5 m/sec and a sharp increase in power requirements at higher airspeeds (Dudley & DeVries 1990). The maximum range speed based on the same power curve would be *ca* 2.5 m/sec; airspeeds of moths in the present study ($\bar{x} = 3.9$ m/sec; Table 1) are likely to substantially exceed these approximations for both the minimum power speed and the maximum range speed. Although power curves have not been determined on individual *U. fulgens* flying over their full range of airspeeds, the high advance ratios calculated for this species (the ratio of forward speed to the mean flapping speed of the wings) suggest that changes in forward airspeed will have pronounced effects on wing aerodynamics and thus on total power expenditure during flight (Dudley & DeVries 1990, Dudley 2000). Considerable uncertainty attends the quantitative features of migratory energetics and optimization criteria used by this species, but *U. fulgens* does appear to be sacrificing energetic efficiency of travel for absolute speed of flight, and thus for migratory duration if the pathway in question is of fixed length. Minimization of time rather than energy during long-distance migration may in any event be more important for short-lived organisms (Baker 1984), particularly if risks of predation are high (see below).

Further support for such postulated insensitivity to migratory flight energetics in *U. fulgens* derives from the absence of compensatory responses to wind speed and wind direction. Migrating *U. fulgens* do not compensate course direction for wind drift (Srygley *et al.* 1996); nor does this taxon adjust airspeed according to varying wind directions (see Results), as would otherwise be predicted by optimal migration theory (Srygley & Oliveira 2001). Similarly, failure to compensate for tailwind drift characterizes migrating *Aphrissa* butterflies (Srygley *et al.* 1996). Females of the butterfly *Phoebis sennae* compensate for tailwinds during migration, but males do not (Srygley 2001), possibly indicating different migratory strategies for the two genders. Nonetheless, only a detailed time and energy budget for migrant animals can evaluate quantitative deviations of flight speed allometries from theoretical optima. As geographical origin, destination, and cumulative energetic expenditure are not known for these migrants, the relative importance of energy- and time-optimization for long-distance flights of these moths must remain speculative. Given the long migratory distances postulated for *U. fulgens* (>1000 km; Dudley & DeVries 1990, Smith 1992), however, some degree of optimization in either flight costs or migratory duration may be expected for this species. The present data are consistent with the latter possibility, but only physiological measurements on the same individual at different stages of the migration can unequivocally test this hypothesis.

Although changes in airspeeds of individual migrants flying over long distances cannot at present be determined for logistical reasons, the possibility of behavioral compensation to variable body mass is amenable to experimental verification via attachment of weights to migrating moths, together with pre- and post-manipulation measurement of airspeeds. In such experiments, effects of handling and possible escape responses must also be evaluated (Oliveira *et al.* 1998). Additional consequences for flight performance may ensue from mass hypertrophy. For example, escape responses from predators may also be degraded due to the effects of lipid loading and increased body mass on flight maneuverability (Hedenström 1992). Experimental additions of mass to nonmigrant butterflies in field contexts have generally resulted in insignificant changes in airspeeds and in recapture probabilities (Kingsolver & Srygley 2000, Srygley & Kingsolver 2000). For nonmigrant bats and birds in laboratory contexts, addition of artificial masses has typically yielded a decline in airspeed (Videler *et al.* 1988, Hughes & Rayner 1991). No

comparable weight-loading experiments have been carried out for migratory insects in either laboratory or field contexts. Such studies should ideally be conducted in natural environments because of potentially constraining effects of enclosure size on flight performance (Srygley & Dudley 1993, Dudley & Srygley 1994, Dudley 2000).

Predation by birds may pose a major risk to long-distance boundary layer migrants. One well-known defense mechanism used by arthropods against predation is unpalatability. Caterpillars of *U. fulgens* sequester potentially toxic polyhydroxy alkaloids from their host plants, various *Omphalea* spp. in the family Euphorbiaceae (Fellows 1986, Kite *et al.* 1990, Smith 1992). As in other unpalatable Lepidoptera, sequestration of toxic compounds by *U. fulgens* larvae likely confers some chemical protection to the adult moths. The relatively slow and predictable flight of *U. fulgens* is also consistent with some degree of unpalatability (Chai & Srygley 1990, Srygley & Chai 1990). Adult *U. fulgens* are in fact usually (but not always) sight- or taste-rejected by a specialized avian insectivore, the Rufous-tailed Jacamar (Chai 1986, pers. comm.). Various reports, however, suggest at least occasional predation by other avian taxa on diurnally migrating *U. fulgens*. Williams (1930) noted an 1871 record of unspecified birds destroying *U. fulgens* during a large migration in Panama. Smith (1992) stated that swallows of the genus *Progne* and *Pheoprogne* regularly chase *U. fulgens*, whereas other avian insectivore such as jacamars and tyrannid flycatchers ignore the moths.

Field observations of attacks by Mangrove Swallows support the claim that *U. fulgens* is palatable to at least a subset of potential avian predators. None of the 25 moths captured in 1987 exhibited damage to the wings and/or body. In 1998, however, almost 30 percent of those moths arbitrarily selected for airspeed measurements were found to have such damage. Damaged female moths from 1998 also had approximately twice the lipid content of undamaged females from the same year, raising the possibility that calorically more valuable prey are being selected by predators. Relative to these female moths, male moths may be avoided by predators altogether, escape attack more effectively, or be captured much more frequently (*i.e.,* rates of unsuccessful attack are very low). Female moths in general express a higher lipid content relative to males, possibly associated with oogenesis (Smith 1992; Table 1); so one explanation may simply be that predators attack prey that provide greater energetic reward, preferring females to males and also selecting females with greater amounts of abdominal lipids. Alternatively, these latter individuals may be more susceptible to attack or may be more capable of escaping following sublethal damage. Further observations, systematic sampling, and quantitative measures of predatory damage through the course of a migratory period will be necessary to determine the overall impact of avian predation on *U. fulgens*.

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