

Optimal strategies for insects migrating in the flight boundary layer: mechanisms and consequences

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Synopsis Directed aerial displacement requires that a volant organism's airspeed exceeds ambient wind speed. For biologically relevant altitudes, wind speed increases exponentially with increased height above the ground. Thus, dispersal of most insects is influenced by atmospheric conditions. However, insects that fly close to the Earth's surface displace within the flight boundary layer where insect airspeeds are relatively high. Over the past 17 years, we have studied boundary-layer insects by following individuals as they migrate across the Caribbean Sea and the Panama Canal. Although most migrants evade either drought or cold, nymphalid and pierid butterflies migrate across Panama near the onset of the rainy season. Dragonflies of the genus *Pantala* migrate in October concurrently with frontal weather systems. Migrating the furthest and thereby being the most difficult to study, the diurnal moth *Urania fulgens* migrates between Central and South America. Migratory butterflies and dragonflies are capable of directed movement towards a preferred compass direction in variable winds, whereas the moths drift with winds over water. Butterflies orient using both global and local cues. Consistent with optimal migration theory, butterflies and dragonflies adjust their flight speeds in ways that maximize migratory distance traveled per unit fuel, whereas the moths do not. Moreover, only butterflies adjust their flight speed in relation to endogenous fat reserves. It is likely that these insects use optic flow to gauge their speed and drift, and thus must migrate where sufficient detail in the Earth's surface is visible to them. The abilities of butterflies and dragonflies to adjust their airspeed over water indicate sophisticated control and guidance systems pertaining to migration.

Introduction

Insects engaging in long-distance displacement via flight face a formidable obstacle in the form of ambient winds. Because wind speed increases exponentially with distance above the ground to a height of several hundred meters (Geiger et al. 2003), a vertical endpoint exists beyond which, for any given insect, ambient winds surpass its maximum airspeed. Displacement above such a height must correspondingly be oriented downwind. This concept, introduced as the flight boundary layer by Taylor (1958), indicates that directed flight is most feasible for insects flying either close to the Earth's surface or within vegetation where ambient winds are low. Typical airspeeds above vegetational canopies well exceed maximum flight speeds for the majority of insect taxa, given their average adult body length of 4–5 mm (Dudley 2000). Much of the insect fauna correspondingly have little opportunity for controlled displacement other than the decision to

initiate flight and subsequently to displace according to atmospheric motions. Although ambient winds can vary substantially in both space and in time, their typically high-relative magnitudes drive the passive aerial dispersal of most insect species (e.g., Westbrook, 2008).

In contrast, larger migratory insects, such as dragonflies, moths, and butterflies, generally engage in continuous wing flapping and active forward motion within the flight boundary layer (Williams 1930; Baker 1978; Walker 1985). Such powered flight generally occurs during the day, as this behavior relies on visual cues both for assessment of groundspeed and for identification of flowers bearing the nectar necessary to sustain high-metabolic rates. For these insects, the higher absolute flight speeds deriving from increased body mass (i.e., 4–8 m/s; Srygley and Dudley 1993; Dudley and Srygley 1994; Dudley 2000) permit flight above forest canopies and over water where ambient winds would otherwise well exceed typical insect flight speeds. Ambient winds

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may augment flight directionality in some cases (Mikkola 1986), but the general pattern is one of persistently oriented displacement over a range of hundreds to thousands of kilometers. Sustained flight during the day exposes insect migrants to avian insectivores as well as to the possibility of significant thermal stress, particularly in the warm tropics. Nonetheless, the positive allometry of animal flight speeds indicates that only larger insects with higher absolute speeds can effectively impose directionality during migratory flight. The evolution of sustained long-distance migratory systems, characteristic of many birds and some bats, is thus feasible for only a much smaller subset of all insects.

Focusing on a suite of migratory Neotropical Odonata and Lepidoptera (Fig. 1), we discuss behavioral and physiological adaptations that are necessary for long-distance migration within the

flight boundary layer. Multiple sensory and locomotory responses are required for effective near-ground navigation within complex aerial landscapes characterized by varying winds. We outline the various mechanisms of wind drift compensation, airspeed adjustment in response to depletion of lipid reserves, and the use of solar and geomagnetic cues during such flight. More broadly, these behaviors must be coordinated if long-distance migratory flight within the boundary layer is to be effective and to evolve. The relative rarity of such behaviors among larger insects may correspondingly indicate intrinsic limits to behavioral complexity relative to their volant vertebrate counterparts. In contrast, studies of insect taxa that do engage in such long-distance flights may reveal novel capacities or outcomes that are of general interest to the field of animal migration.

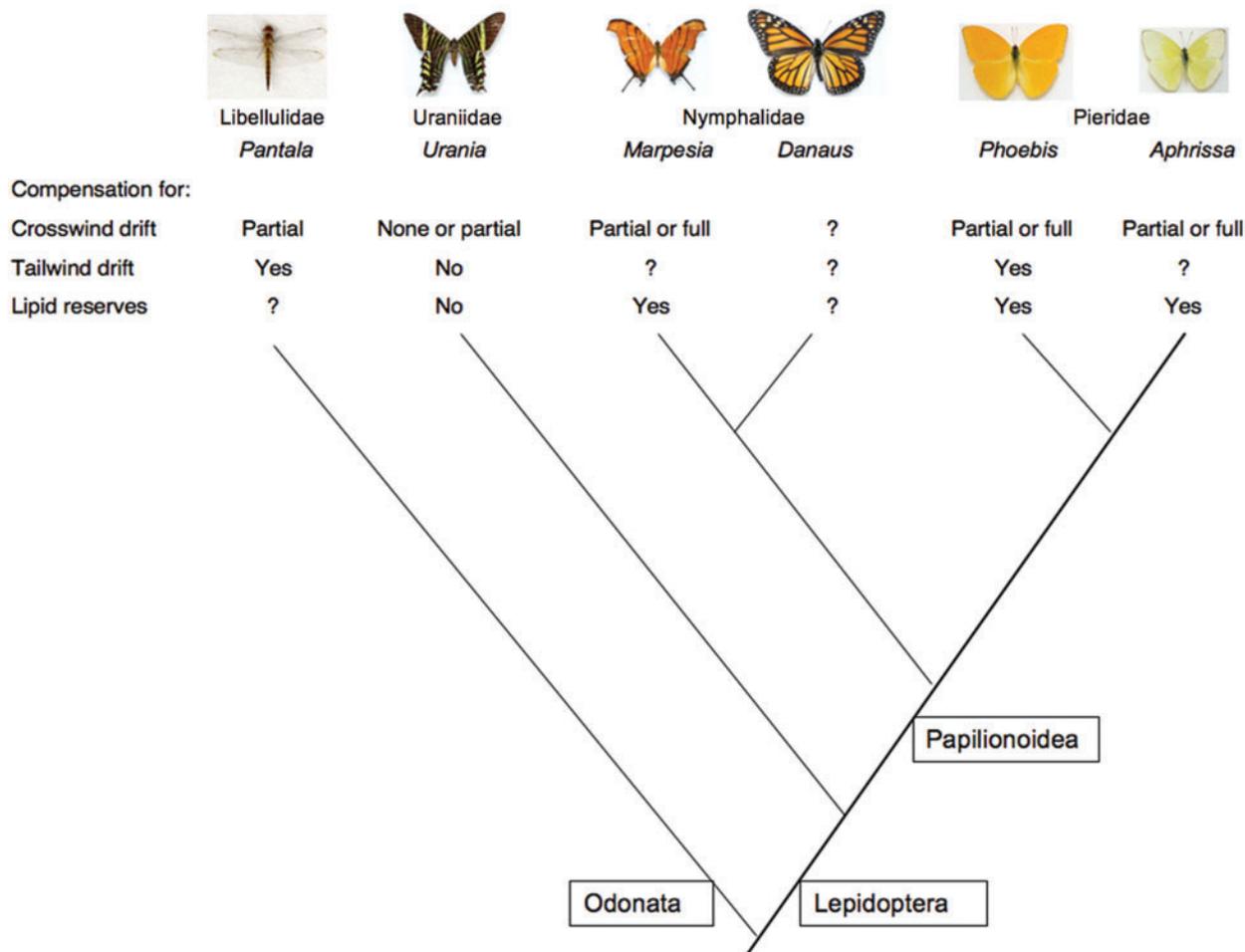


Fig. 1 Phylogenetic relationships among the migratory dragonfly, moth, and butterfly genera of interest, with a photograph of a representative species from each genus. Relationships of the genera within Nymphalidae are based on Wahlberg et al. (2003), and relationships among lepidopteran families are based on Wahlberg et al. (2005). Results from the compensation studies are summarized beneath each genus with a question mark indicating a need for future research in the designated taxon.

Orientation studies and migratory routes

From March to August, at least 10 butterfly species and 2 moth species migrate across Lake Gatún, a large body of water through which runs the Panama Canal (Fig. 2). Because of their abundance, we have largely focused on 3 pierids (*Aphrissa statira*, *A. boisduvalii*, and *Phoebis argante*), 3 nymphalids (*Marpesia chiron*, *M. petreus*, and *Historis acheronta*), and the day-flying moth, *Urania fulgens*. Between 1992 and 1995, we mapped the migration flyway of *A. statira* across the Isthmus of Panama (Fig. 2, also see maps in Srygley et al. 1996; Srygley and Oliveira 2001a). Simultaneous sampling at Barro Colorado Island and along the Colombian coast in 1996 indicated that the migration of *A. statira* in Colombia might contribute to the migratory population in Panama, but simultaneous sampling the following year during the migratory peak in Panama demonstrated that Colombia was not the origin of the migration across the Isthmus of Panama (Srygley and Oliveira 2001a). Other migrating butterfly species exhibit similar directional orientations over the Panama Canal (Table 1). Thus, all of the butterfly species are on tracks to

move from the Atlantic wet forest to the Pacific dry forest following the onset of the rainy season.

In contrast, the migrations of the moth *U. fulgens* across the Isthmus of Panama are difficult to predict from year to year. After the migration of numerous individuals in October 1988, we did not again observe migrating *U. fulgens* until December 1994. In only 6 of the subsequent 12 years did *U. fulgens* migrate through our study area (Table 2). With the exception of August 2003, when moths were flying in 2 diametrically opposed directions, they appear to fly southwesterly with the trade winds during the dry season (February–April) and northeasterly in the rainy season (August–October). Their directionality is relatively inconsistent during May–July, and migrations are uncommon from December to February. These displacements in Panama are part of a massive migration of *U. fulgens* across its range, from Veracruz in Mexico to Ecuador (Williams 1930). Data on orientations across this large spatial scale are sparse, but Smith (1983, 1992) attempted to characterize these migrations from scattered scientific accounts, newspaper articles and personal communications. He reported a general southeasterly movement from August to October (Smith 1983). Thus, the flyway is oriented southeast from Mexico to

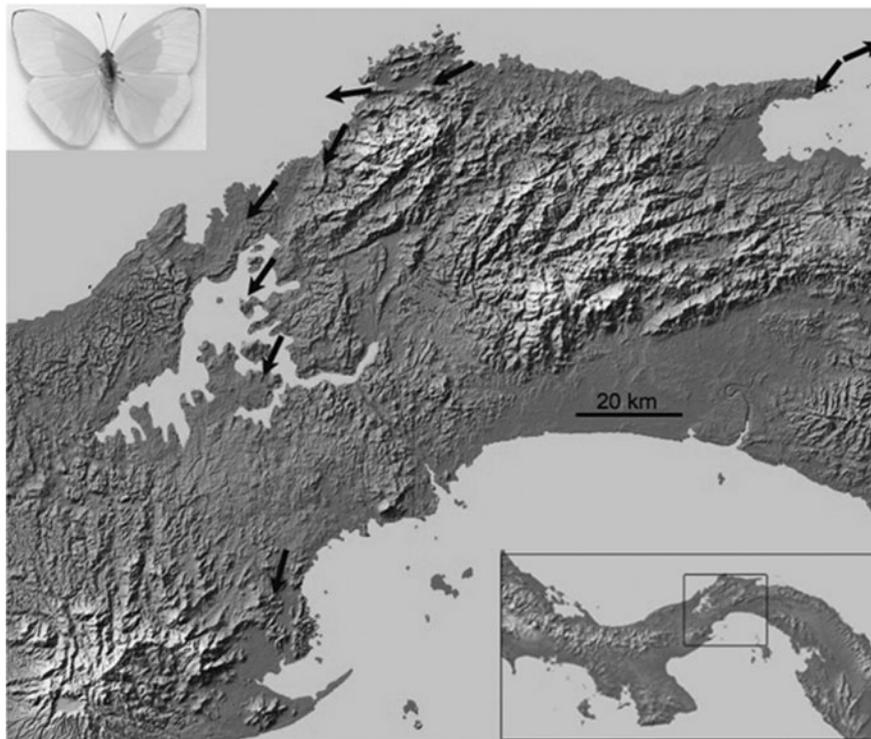


Fig. 2 The annual migration of *Aphrissa* butterflies across the Isthmus of Panama from the wet Atlantic coastal forest to the dry Pacific coastal forest. At each of 8 locations, arrows represent the mean orientations of butterflies ($n > 20$ at each location). Magnetic and geographic North are towards the top of the page. Inset: topographic map of Panama with the enlarged view of the isthmus and Lake Gatún designated by a rectangle. The depicted butterfly is a male *A. statira*.

Table 1 Morphological data, airspeeds, and directional headings for diurnal migratory Lepidoptera in central Panama

Species	Gender	Wet body mass ^a (mg)	Wing loading ^a (N/m ²)	Lipid content ^a (% wet mass)	Airspeed ^a (m/s)	Migratory direction ^b (°)
<i>Aphrissa boisduvalii</i>	Female	201	1.07	12.4	5.0	211
	Male	187	1.06	7.9	4.8	
<i>Aphrissa statira</i>	Female	180	1.12	10.0	4.6	210
	Male	200	1.14	10.3	5.2	
<i>Marpesia chiron</i>	Female	136	1.07	15.4	4.5	227
	Male	106	0.81	8.7	3.7	
<i>Marpesia petreus</i> ^c	(Pooled)	196	1.08	15.6	4.6	228
<i>Hisotris acheronta</i>	Female	480	2.30	10.6	6.5	236
	Male	543	2.24	9.6	6.6	
<i>Phoebis argante</i>	Female	252	1.06	7.8	4.6	210
	Male	214	0.93	11.5	4.9	
<i>Urania fulgens</i>	Female	490	2.73	15.0	3.8	See Table 2
	Male	303	2.23	12.6	3.9	

^aData from Dudley et al. (2002); Dudley and Srygley (2008).

^bData from Srygley et al. (1996). Not separated by gender.

^cSexes pooled because of low sample size for males.

Table 2 Orientation^a of *Urania* and the maximum migratory rate (MRR)^b in each calendar quarter on Lake Gatún, Panama.

Year	February–April		May–July		August–October		November–January	
	Orientation	MRR	Orientation	MRR	Orientation	MRR	Orientation	MRR
1994							Southwest	
1995	216°	25			40°			
1996	Southwest	5						
1998			Northeast	23	18°	>300		
2002			1° & 181°	6				
2003			79–90°		79° & 259°			
2005					Northeast	75		
2006			50° & 230°	60				

^aOrientations to 8 compass points indicate general orientations during censuses; values expressed in degrees indicate mean orientations of the population calculated with circular statistics. *Urania* were not observed migrating during 1996, 1997, 1999, 2000, 2001, or 2004.

^bMRR is the number of *Urania fulgens* crossing a 300 m transect over Lake Gatún per minute.

Costa Rica, until it reaches the east–west oriented Panamanian land bridge to South America. Perhaps somewhere near the Panama Canal, the flyway shifts to northeasterly across the isthmus. Smith (1983) noted that return migrations to the north and west (as we have observed to the south and west across the Isthmus of Panama) may occur in the dry season following migrations from August to October. In agreement with his observations, there was no dry-season migration in some years (e.g., 2005 and 2006). However, our data for other years (e.g., 1995 and 1998) clearly indicate that the dry-season migration preceded the migration during the wet season. Focusing on both ultimate and proximate factors resulting in bidirectional, as opposed to

unidirectional, migrations may be a more useful approach toward understanding the ecology and physiology of migratory orientation in *U. fulgens*.

Among dragonflies, the spot-winged glider *Pantala hymenaea* migrates east to northeast over the Panama Canal (Srygley 2003). The association of *Pantala* with monsoons and other frontal systems has been noted over the Panama Canal (Srygley 2003) and elsewhere (Dumont and Verschuren 1991; Russell et al. 1998). Dumont and Verschuren (1991) hypothesized that these dragonflies use the leading edge of storms to forecast newly formed ephemeral pools in which they reproduce.

Dragonflies, *Urania* moths, and butterflies all fly in the daytime and near the surfaces over which they

Taxon	Compensation (95% C.L.)	Predictions supported	Mechanisms supported
<i>Pantala</i> dragonflies 	54% (35%, 72%)	Partial compensation	Ground reference
<i>Urania</i> moths 	12% (-69%, 93%)	No compensation or Partial compensation	No reference or Ground reference
Nymphalidae & Pieridae butterflies 	114% (63%, 165%)	Partial compensation or Full compensation	Ground reference or Use of landmarks

Fig. 3 Compensation for crosswind drift and its supportive mechanisms based on the 95% confidence intervals for regression of change in heading versus change in angle of wind drift. Results for butterflies and moths are from Srygley et al. (1996), and those for dragonflies from Srygley (2003).

migrate. The insects maintain their characteristic height over vegetation, terrain, and open water (see Fig. 1 in Srygley and Oliveira 2001b). We have found these boundary-layer fliers to be particularly useful for assessing individual responses to both natural and experimental perturbation. We intercept individual, naturally migrating insects over the Panama Canal or Caribbean Sea and follow them alongside at an even pace with a motorized boat; we have never discerned behavioral alterations to flight trajectory in response to being followed at these distances (2–3 m). We then measure the insect's airspeed and orientation with either unidirectional anemometry and a sight compass (Dudley and DeVries 1990) or conventional sailboat navigation equipment (Srygley 2001a, 2001b, 2003). Ambient climatic conditions can be measured intermittently by stopping the boat (Srygley et al. 1996) or recorded simultaneously (Srygley 2001a, 2001b, 2003). The insect is then captured to verify its identification and to measure morphological features relevant to flight. This general method has been used to investigate whether these insects maintain direction in varying winds (both with and without landmarks), and whether they adjust airspeed in accordance to that predicted to use minimal fuel.

Compensation for crosswind drift

The atmosphere is stoked by heat derived from the sun, generating winds that an insect encounters as it flies across the landscape. In instances such as the trade winds on a synoptic scale, they are often predictable in location, time, direction, and magnitude, but more typically winds are variable in direction and force. Crosswinds cause an insect to

drift off the straight-line path defined by its preferred heading. A migratory insect's response to crosswind drift depends in part on its capacity to perceive wind drift, to re-orient appropriately, and to fly sufficiently fast to compensate for detrimental winds. Whether an insect is prone to drift or adjusts its heading to compensate for crosswinds and maintain its track is an important feature of migration. Without wind-drift compensation, an insect cannot maintain a preferred track across a landscape, which is the essence of migration (Kennedy 1985). Drift compensation is particularly important in narrow geographical formations of suitable habitat, such as the Panamanian land bridge, where inability to compensate may result in being blown out to sea.

We have measured crosswind drift compensation in migratory butterflies, *Urania* moths, and *Pantala* dragonflies as they cross Lake Gatún and the Panama Canal (Fig. 3). Drift compensation over bodies of water is particularly difficult because landmarks on shores may be too distant to see. At the site where we conducted these studies, Lake Gatún is about 1.5 km across. As migratory butterflies flew across the lake and encountered winds that altered their tracked direction by varying degrees of drift, they compensated in ways that matched the change in angular orientation (Srygley and colleagues 1996). As a result, butterfly tracks do not differ from their original track direction despite variable crosswinds (Srygley and Oliveira 2001a). On average, the butterflies showed full compensation for wind drift, although variation among individuals did not exclude the possibility of partial compensation (minimum of 63%) or over-compensation (maximum of 165%); these minima and maxima are derived from the 95% confidence limits. In contrast to butterflies, *Urania* moths did

not change their heading to match change in the extent of wind drift as they crossed Lake Gatún (Srygley et al. 1996). As a result, *Urania* tracks drifted downwind with very little, if any, compensation (on average 12%, Srygley and Oliveira 2001a). However, due to variation among individuals, the possibility for partial compensation (up to a maximum of 70%) cannot be excluded. Drift compensation in *Pantala* dragonflies averaged 54%, with a range from 35% to 73% (95% confidence limits, Srygley 2003). Thus, *Pantala* dragonflies demonstrated partial, but significant, compensation when crossing Lake Gatún.

A flying insect may maintain a straight-line route by an optomotor response to the apparent motion of a ground reference (Kennedy 1985), which is perceived as the optic flow of surface features across the insect's compound eyes (Franceschini et al. 2007). Over solid terrain, honey bees (Heran and Lindauer 1963), bumblebees (Riley et al. 1999), and desert locusts (Preiss and Gewecke 1991) all correct for the perception of drift, relative to the substrate below, by heading upwind. When using this method over water, however, insects underestimate drift caused by wind, because the water surface also moves downwind, albeit more slowly. Thus, partial compensation in *Pantala* dragonflies is evidence for use of this optomotor response to drift. Full compensation for crosswind drift requires the use of at least one visible landmark on the shore that serves as a beacon, while orienting towards it with a compass. However, mechanisms exist to compensate without a compass, including the use of 2 landmarks maintained in a line of sight, and the use of 2 lateral landmarks that are held in parallax. The ability of butterflies to compensate fully when crossing Lake Gatún suggests that they use one of these mechanisms. When followed over the Caribbean Sea in the absence of terrestrial landmarks, *Phoebis sennae* butterflies could sometimes partially compensate for wind drift. Without visible terrestrial landmarks, butterflies relied on the motion of a ground reference to compensate for drift (Srygley 2001a).

Celestial and magnetic compasses

A migrating insect may maintain its heading with inner compasses that sense a global reference such as the sun, celestial skylight, or the Earth's magnetic field. In order to maintain a constant heading using the sun for orientation, the migrating insect must use a biological clock to gauge time of day and to compensate for changes in the sun's position. Using clock-shift experiments, we demonstrated use

of a time-compensated sun compass for orientation by the pierid butterflies *A. statira* and *P. argante* (Oliveira et al. 1996, 1998). Following a 4 h advance of the endogenous clock, the shift in orientation averaged 91° and 83° for *A. statira* and *P. argante*, respectively. The most effective use of the sun as a compass would require full compensation for the daily movement of the solar azimuth, for which the predicted shift in orientation was 120°. Errors about the mean orientations as defined by the 95% confidence intervals did not exclude the hypothesis that both butterfly species compensated fully for time. Alternatively, migrating insects might apply more robust rules in approximating the position of the sun, such as averaging the sun's positional changes over the course of the day (about 15° per hour) or by using a step-function that approximates the sun's position as easterly in the morning but shifting abruptly westerly in the afternoon (Dyer and Dickinson 1994). Under these more robust methods of time compensation, the predicted shift in orientation is 60° for a time-average and 180° for a step-function. The errors about the mean orientations for both butterfly species excluded the use of a step-function to approximate the sun's position, but failed to eliminate the hypothesis of time-averaging (Srygley and Oliveira 2001b). Using monarch butterflies (*Danaus plexippus*) that were tethered and flown in an orientation apparatus, Mouritsen and Frost (2002) clock-shifted individuals with a 6 h advanced treatment and a 6 h delayed treatment. The shift in orientations was 89° on average for the time-advanced treatment, and 110° for the time-delayed treatment. Similar to our results for pierid butterflies, errors about the means for monarch butterflies rejected a step-function mechanism but failed to reject either time-averaging or full compensation for the relative motion of the sun.

Skylight is polarized perpendicularly to the plane defined by the observer, the sun, and the observed point of the sky (for a recent review, see Horváth and Varjú 2003). Desert locusts are sensitive to polarized light (Homberg 2004; Mappes and Homberg 2004). Whether or not monarch butterflies use polarized skylight as a migratory orientation cue is controversial. They cease flying when the ultraviolet band (UV: <394 nm) of sunlight is blocked (Froy et al. 2003). Thus, stimulation of a UV photoreceptor is required for sustained flight, and the ommatidia on the dorsal rim of the compound eyes are anatomically specialized for detecting polarized light (Reppert et al. 2004), but are sensitive only to UV wavelengths (Sauman et al. 2005). When a polarizing filter placed over a flight arena

is rotated 90°, tethered monarch butterflies also rotated the axis of their body in the same direction. Orientations became random when a filter blocked polarized light in the UV range, and were restored when the filter was removed. In some instances (Reppert et al. 2004; Sauman et al. 2005), orientation was restored 180° from the initial orientation, indicating an axial orientational response to the linear axis of the artificially polarized light. Stalleicken et al. (2005) tested the ability of monarch butterflies to orient when the sun was visible but with the dorsal-rim ommatidia covered with opaque paint. Butterflies subjected to a 6 h advance clockshift oriented 86° clockwise relative to control butterflies, although they were unable to detect polarized skylight. Thus, the sun and polarized skylight compasses may be autonomous. Carefully designed experiments with potential conflicts between information gathered from the sun and polarized skylight need to be conducted to evaluate how migrating insects integrate these celestial cues.

The geomagnetic field is a reliable source of directional information, and may be particularly relevant when and where a celestial compass is inaccurate. For example, polarized skylight does not penetrate completely overcast skies, and more than half of the sky must be visible for it to provide unambiguous directional information (Rossel and Wehner 1986; but see Pomozi et al. 2001 for a description of the polarized light pattern under partly cloudy skies). In addition, partial compensation for the variable motion of the tropical sun's azimuth results in error, and yet full compensation requires that the insect possesses an accurate ephemeris function for solar location and the time of year. Moreover, the tropical mid-day sun is nearly overhead, making detection of the azimuth's angular motion even more difficult. Despite these challenges, migrating *A. statira* and *P. argante* butterflies maintained a single orientation route over the course of a day (Oliveira et al. 1998), which can only be achieved by either fully compensating for the relative motion of the sun or using the Earth's magnetic field as a reference. Further observational support for a magnetic compass in migratory pierid butterflies came from a release experiment that we conducted on the Panama Canal (Srygley et al. 2006). *Aphrissa statira* individuals that were captured flying over Lake Gatún and then released under an overcast sky the following day maintained their original migratory direction. This result, as well as the abilities of other migratory butterflies (Schmidt-Koenig 1985; Gibo 1986), *Urania* moths, and dragonflies (R.B.S. and R.D., personal observation)

to maintain a preferred compass orientation under completely overcast skies, suggest that the Earth's magnetic field may serve as an orientation cue.

To investigate whether *Aphrissa* butterflies use a magnetic compass for orientation, we conducted 2 perturbation experiments (Srygley et al. 2006). In the first one, we disrupted the butterfly's magnetic sense with a brief but strong magnetic field applied to each insect. Each experimental butterfly, or an identically handled control, was then released over the Panama Canal. As predicted, experimental butterflies had a more dispersed pattern of orientation than did controls. The average direction adopted was northeasterly, 160° anticlockwise to the natural migratory direction, whereas the control butterflies adopted 2 diametrically opposed orientations, either shifted 33° clockwise or 147° anticlockwise to the migratory direction. Control and experimental butterflies differed in that some controls headed in the prevailing migratory direction. In the second experiment, we obstructed sun compass cues and reversed the polarity of the local magnetic field to position magnetic north towards geographic south. Each experimental butterfly was released into a flight arena within the manipulated field. Control butterflies were handled identically except that they were released into a flight arena within the natural magnetic field. As predicted, experimental butterflies experiencing the reversed magnetic field oriented on average 180° opposite to their natural migratory direction. Control butterflies oriented both towards and 180° away from the natural migratory direction. These differences between controls and experimentals support the hypothesis that they possess a sense for magnetic orientation. The axial orientations of the control butterflies in both experiments were probably due to escape responses towards the sun (Froy et al. 2003). A similar proportion of the experimental butterflies probably had the same motivation to escape. Ideally, the abilities of migrating butterflies, *Urania* moths, and dragonflies to orient with magnetic compasses should be tested under fully overcast skies. Otherwise, experiments should be planned carefully to decouple orientations predicted from the treatments from inadvertent responses resulting from the experimental setup (i.e. the positive phototaxis that characterizes many insects).

Tailwind drift compensation

Flight is a costly activity, per unit time, relative to either running or swimming. For flying animals in general, the functional dependence of the cost of

locomotion on airspeed increases from a minimum defined by the minimum power velocity to form either a J-shaped or the right-hand half of a U-shaped power curve. Unfortunately, we do not know how metabolic costs for any migratory insect change with airspeed. For *U. fulgens*, however, a shallow U-shaped curve relating mechanical power expenditure to forward airspeed has been postulated (Dudley and DeVries 1990). The high forward flight speeds relative to the mean flapping speed of the wings for the migratory butterflies listed in Table 1 suggest similarly shaped power curves (Dudley, 2000). The aerodynamic power curve for the dragonfly *Sympetrum sanguineum* is also distinctly J-shaped (Wakeling and Ellington 1997). Although transduction of metabolic power to useful mechanical work may occur at variable efficiencies according to the timing and intensity of muscular contraction, it is likely that choice of flight speed has a considerable influence on the rate of energetic expenditure for long-distance boundary-layer migrants.

Optimal migration strategies derive from theoretical predictions based on either the U-shaped or J-shaped power curve. Four clearly defined velocities may be adopted by a migrant to optimize different aspects of its time and energy budgets. The minimum power velocity (V_{mp}) maintains the animal aloft for the longest period, and the maximum range velocity (V_{mr}) maximizes distance for a minimum required energy. Maximum velocity (V_{max}), which is limited by the power available for flight, minimizes flight time to the destination site when there is no feeding en route. When time for energy deposition is budgeted, the minimum time velocity, V_{mt} is $<V_{max}$ and is $>V_{mr}$ (Alerstam and Hedenström 1998; Srygley and Oliveira 2001b). Srygley and Oliveira (2001b) reviewed general models for flight optimization and discussed constraints that might be important when adapting optimal migration theory to insects.

In still air, the airspeed that minimizes power per unit distance and maximizes an animal's migratory range can be determined by drawing a tangent to the power curve through the origin. Because V_{mr} is based on groundspeed, the addition of a tailwind to the airspeed of an insect would decrease the optimal velocity that the insect should adopt. Similarly, the addition of a headwind would result in an increase in the insect's V_{mr} . If the insect is not adjusting for winds, then airspeed would remain steady and groundspeed would increase linearly with tailwind speed.

Animals that migrate in the flight boundary layer are particularly amenable to testing optimal migration strategies because 2 of the 3 vectors relevant to tailwind drift compensation (the organism's airspeed and heading, groundspeed and track, and ambient wind speed and direction) may be collected simultaneously and the third calculated by vector analysis. We followed migrating *P. sennae* butterflies as they flew over the Caribbean Sea from the Colombian coast towards Panama. As predicted from optimization of migratory range, female butterflies slowed their airspeed in a tailwind and increased it in a headwind (Srygley 2001b). In contrast, males did not adjust their airspeed for tailwind drift. Females may minimize energy consumption to conserve lipids for eggs, whereas males may minimize the time to the destination site in ways that maximize the opportunities for mating with newly arrived or newly emerged females. In contrast to the pierid butterflies, neither female nor male *U. fulgens* moths adjusted airspeed for tailwind drift (Dudley et al. 2002).

A more refined model incorporating simultaneous adjustment for tailwind and crosswind drift may be applied when the flying animal compensates for crosswind drift (Liechti et al. 1994). In this model, an organism behaving optimally for maximizing range should alter airspeed as drift increases (in proportion to the inverse of the cosine of the drift angle), above and beyond the increase in airspeed needed to compensate for tailwinds (as measured by the difference between groundspeed V_g and airspeed V_a). To test this effect, Srygley (2003) calculated tailwind as the incremental effect of wind (i.e., $V_g - V_a$) and evaluated airspeed as a stepwise regression on tailwind speed and on the inverse of the cosine of the drift angle. Individual *Pantala* dragonflies migrating across the Panama Canal adjusted their airspeed accordingly for tailwind drift. Airspeed was not associated with crosswind drift ($P=0.119$) following adjustment for tailwind drift ($P<0.0001$). Thus, dragonflies did not simultaneously adjust their airspeeds for both tailwinds and crosswind drift, at least in this analysis.

Shamoun-Baranes et al. (2007) criticized studies of optimal migration that use the standard method of calculating tailwinds as groundspeed is less than the airspeed (the incremental effect of wind). These authors demonstrated that calculating tailwind velocity without taking into account the angular difference between the wind direction and the track of the bird can lead to a significant correlation between airspeed and tailwind speed, when in fact no such correlation exists. In our studies of migrating insects, we typically decomposed ambient winds into the

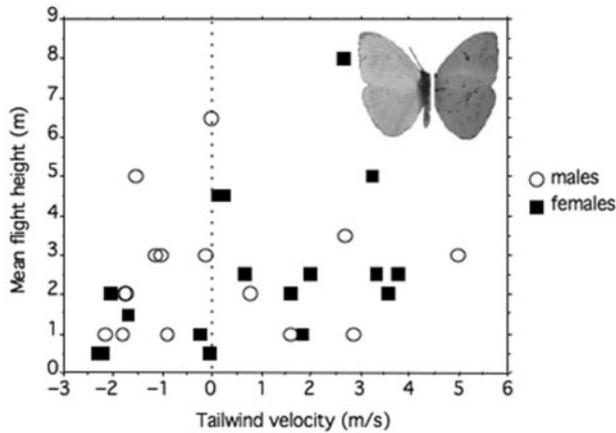


Fig. 4 Mean height above water relative to mean tailwind velocity for *P. sennae* males and females migrating over the Caribbean Sea. The depicted butterfly is a *P. sennae* male showing the dorsal (left) and ventral (right) side of the wings.

components of tailwind and crosswind drift (Srygley 2001b; Dudley et al. 2002; Srygley 2003), or we excluded winds that were not oriented within 5° of the body axis (Srygley et al. 1996). For dragonflies, a comparison of results from airspeed regressed on the incremental effect of wind with those from airspeed regressed on the tailwind drift component of the wind vector resulted in no qualitative differences (Srygley 2003).

As wind speeds increase, the flight boundary layer thins. In favorable winds, insects may enhance their effect by flying higher, whereas they may minimize the effect of headwinds by flying closer to the Earth's surface (Kennedy 1951). Franceschini et al. (2007) developed the early model of Kennedy (1951) into an optic feedback model, whereby the angular velocity of a point directly below the insect equals the ratio between groundspeed and height of flight. By this mechanism, an insect sensing a reduction in groundspeed decreases its altitude in ways that hold optic flow speed constant across the compound eyes. We estimated the altitude of *P. sennae* butterflies flying over the Caribbean Sea, and our results show a sexual difference in this form of drift compensation, as well. Among females, altitude was positively correlated with tailwind velocity (Spearman's rank correlation, $\rho = 0.60$, $n = 17$, $P = 0.016$), whereas that of *P. sennae* males was not correlated with tailwind velocity ($\rho = 0.22$, $n = 15$, $P = 0.40$; see Fig. 4). It is important to note that the model of Franceschini et al. (2007) results only in a change in altitude that maintains optic flow constant. Groundspeed decreases in proportion to altitude, but airspeed does not change (e.g., it does not increase in a headwind). Thus, their optic-flow regulator model

does not explain the compensation for tailwind drift that we observed in *P. sennae* butterflies and *Pantala* dragonflies.

The dragonfly *Pantala hymenaea* regularly engages in stereotypical lateral movements when flying across the Panama Canal (R.B.S., personal observation). These lateral shifts of ca. 1–3 wingspans in the otherwise rectilinear forwards trajectory do not appear to be escape responses because: (1) there is no measurable change in mean orientation before and after measurements, (2) lateral shifts are not instigated by our approach, and (3) dragonflies always return to a steady forwards motion after shifting. In honeybees, altitude control is affected when cues to transverse optic flow are removed, whereas it remains unaffected by removal of cues to longitudinal optic flow (Baird 2007). Thus, stereotypical lateral movements may be used to assess altitude independent of groundspeed. Assessment of altitude with transverse optic flow would then allow the insect to independently modulate groundspeed and altitude when perturbed by winds (Beyeler and colleagues 2007), such as is observed during compensation for tailwind drift.

Energy reserves and the costs of migratory flight

Migratory lepidopterans typically engage in substantial premigratory lipid accumulation as well as regular nectar feeding en route (Williams 1930, Johnson 1969; Brown and Chippendale 1974; Walker 1985; Gibo and McCurdy 1993; Malcolm and Zalucki 1993; Brower et al. 2006), and our diurnal lepidopteran migrants in central Panama are no exception. Abdominal lipid reserves of *U. fulgens* captured during migration range from 12% to 16% body weight (DeVries and Dudley 1990) and comparable values characterize our suite of Panamanian butterflies (Dudley and Srygley 2008). Net reduction of body mass through oxidation of these lipids may induce compensatory changes in flight speed if migratory energetics were to be optimized (Pennycuik 1969, 1978). In particular, airspeed should vary directly with the square root of body mass if individuals maximize the distance traveled per unit energy expended; wing and body dimensions are assumed to be constant. Although lipid content cannot be measured repeatedly on the same individual, it is possible to compare airspeeds and lipid reserves for multiple individuals sampled from within a migratory event, and to use multivariate statistics to control for the confounding covariate of body mass.



Species	Sex	N	Partial correlation
<i>Phoebis argante</i>	Male	29	0.32 (P<0.001)
<i>Marpesia chiron</i>	Female	24	0.33 (P<0.001)
<i>M. petreus</i>	Female	18	0.43 (P<0.001)
<i>Aphrissa statira</i>	Male	16	0.42 (P<0.001)
<i>A. boisduvalii</i>	Female	14	-0.16 (n.s.)
<i>Urania fulgens</i>	Female	50	0.22 (n.s.)
<i>U. fulgens</i>	Male	19	0.18 (n.s.)

Fig. 5 Compensation of airspeed for lipid load following adjustment for body mass in butterflies and *Urania* moths. Results for butterflies are from Dudley and Srygley (2008), and those for moths from Dudley et al. (2002). The dorsal view of a representative species is depicted to the left of each genus.

We have tested airspeed correlates of lipid depletion for the moth *U. fulgens* and for many of the migratory butterfly taxa listed in Table 1 (Fig. 5). In moths, no reduction in flight speed is evident as relative lipid mass declines (Dudley et al. 2002). Migratory butterflies, in contrast, exhibit significantly positive correlations between relative lipid content and airspeed when the effects of overall body size are incorporated (Dudley and Srygley 2008). These differing responses between the phylogenetically basal moth species and the more derived butterflies (Papilionoidea) are mirrored by their relative abilities to compensate for wind drift, as discussed earlier. Optimization of energetic expenditure during flight is likely to be important for long-range displacement in both groups, given their substantial investment in lipids (Table 1), postulated migratory distances on the range of hundreds of kilometers, and the high metabolic costs of flapping flight (Dudley and DeVries 1990; Dudley 2000). Although additional factors may influence patterns of lipid depletion, such as the rate of energetic uptake during migration and duration of premigratory accumulation of energy reserves (Alerstam and Lindström 1990; Hedenström and Alerstam 1995), these comparative results for the moth *U. fulgens* and for migratory butterflies suggest an intrinsically more efficient ability in the latter group to effect long-distance flight. Unfortunately, no information is available on either endogenous lipids or the energetic costs of flight in migratory dragonflies (Fig. 1).

In addition to influencing the costs of flight, additional biomechanical outcomes may derive from variable patterns of lipid deposition. Susceptibility to avian predators may be increased with a higher overall mass via reduced accelerational capacity and increased rotational moments of inertia of the body,

thereby slowing rotational capacity and evasive maneuvers (Srygley and Chai 1990; Srygley and Kingsolver 2000). The ecological impact of predation is not known for lepidopterans migrating within the flight boundary layer, although *U. fulgens* with sublethal predatory damage were also characterized by relatively higher abdominal lipid content compared to their undamaged counterparts (Dudley and colleagues 2002). We have intermittently observed attacks on free-flying *U. fulgens* and the migratory butterflies listed in Table 1 by Mangrove Swallows (*Tachycineta albilinea*) and Grey-breasted Martins (*Progne chalybea*) over Lake Gatún. Diurnal Lepidoptera may be particularly vulnerable to predators when seeking nectar at flowers. Defenses available to diurnal butterflies and moths include increased flight speeds, enhanced maneuverability, and unpalatability to would-be predators (Chai and Srygley 1990; Srygley and Dudley 1993; Dudley et al. 2002). The moth *U. fulgens* is rather slow flying and is chemically defended by alkaloids sequestered from its *Omphalia* host plants (Kite and colleagues 1991); the migratory butterflies are palatable and characterized by fast and erratic flight paths, the magnitude and intensity of which increase following failed attempts to capture them. The costs of such behaviors, although temporally infrequent, are potentially high and would further impinge negatively on the energetics of migration.

Visual orientation during migratory flight

Boundary-layer migrants fly close to the surface of the earth, transiting both the complex topography of vegetational canopies as well as stretches of open water on various spatial scales. Information from the

surrounding visual flow field (and primarily the ventral region) is thus potentially available to gauge their speed and drift relative to a preferred flight vector. Flight at a constant groundspeed based on visual cues in the environment enables horizontal fluctuations in ambient wind velocity to be effectively buffered (Kennedy 1951; Heran 1955, 1956; David 1982; Riley and colleagues 1999; Preiss and Gewecke 1991). For example, foraging honeybees increase airspeeds when flying in a headwind and similarly decrease airspeed in tailwinds (von Frisch and Lindauer 1955; Heran and Lindauer 1963). Such optomotor sensing is an important mechanism by which migrating insects can assess and compensate for the effects of adverse winds. Flight at a constant groundspeed also provides a useful calibration for the absolute distance traveled; foraging honeybees integrate optical flow velocities over time to estimate their cumulative distance of flight (Esch and Burns 1996; Srinivasan et al. 1997; Tautz et al. 2004). More generally, drift induced by movement of air orthogonal to the direction of flight can be detected using the optical flow field, and be correspondingly used to correct for deviations in lateral course (David 1986). These abilities likely characterize all migratory insects, but may be particularly enhanced for boundary-layer migrants with dense optic-flow information in the ventral visual field.

Relative to the moth *U. fulgens*, the abilities of migratory butterflies and dragonflies to adjust their airspeeds over water suggest more sophisticated navigational mechanisms (Fig. 1). Evidence for drift compensation in the complete absence of landmarks over the Caribbean Sea indicates further that migratory butterflies use optic flow to gauge drift when landmarks are not visible (Srygley 2001a). When crossing Lake Gatún in central Panama, however, the opposite shore is potentially visible to flying insects and could provide landmarks for more effective correction of drift. This comparison suggests that migrating *U. fulgens* moths use neither landmarks nor optic flow to maintain azimuthal orientation, at least when flying over water. These distinctive moths are diurnal fliers, whereas migratory moths tend more typically to be nocturnal and to fly at times and heights for which the use of optic flow may not be possible (see Westbrook, 2008). Hence, the inability of *U. fulgens* either to adjust its heading for crosswinds, or to alter airspeed in response to variable fuel load and to tailwinds, may simply reflect plesiomorphic traits generally representative of moths. In contrast, butterflies are derived within Lepidoptera and appear to have evolved, more sophisticated navigational

mechanisms, relative both to drift and to airspeed selection, that underpin long-distance migration. It would certainly be interesting to confirm that *Danaus* butterflies share the navigational mechanisms that we observed in other nymphalid and pierid butterflies. However, the flight of distasteful *Danaus* is slower and the flight apparatus is not as robust as in the palatable butterfly species that we have investigated in the tropics (Dudley and Srygley 1994). It may be that *Danaus* must adopt other means by which to minimize energetic costs during long-distance migration. For example, the monarch butterfly can gain altitude in thermals and soar on favorable winds in southwards autumnal flights, in addition to displacing within the flight boundary layer (Gibo and Pallett 1979; Gibo 1981, 1986).

Future directions

Butterflies and other diurnal Lepidoptera migrating within their flight boundary layer represent an outstanding opportunity for evaluating underlying features of orientation, navigation, and locomotory energetics. When flying low over water, individual migrants can be tracked from a boat, filmed, and then captured, permitting a diversity of physiological analyses to be carried out with little or no perturbation. Flight speeds of these free-flying insects are consistently above those achieved by the same species in wind tunnels and insectaries (Srygley and Dudley 1993; Dudley and Srygley 1994). Spatial and temporal variation in the performance of such free flight, together with measurement of morphological parameters, can also be studied over the course of a migratory period. Linkage of physiological performance with censuses and climatic data then permits an assessment of the implications of particular flight behaviors for migratory outcomes over greater spatial scales. In central Panama, boundary-layer migrants flying over Lake Gatún have provided such a natural laboratory for over 2 decades.

Technological advances should improve our ability to track migrating insects over long distances. Radar systems used to track short-distance flights (Riley et al. 1999) may be applied to long-distance migrants, as well. Radio-tagged insects may also be tracked with radio receivers mounted on motorized vehicles (Wikelski et al. 2006) or potentially low-orbiting satellites (Wikelski et al. 2007). Both of these systems, however, are hampered by the need to capture the insect, attach a radio transmitter, and release it, which may have undesirable behavioral effects due to handling and weight-loading (Srygley and Kingsolver 2000; Srygley et al. 2006). Isotopic

analysis (Rubenstein and Hobson 2004) and assessment of attached pollen (Hagler and Jackson 2001) as indicators of geographical origins can provide information complementary to that derived from in-flight studies for a comprehensive picture of migrant behavior. Comparative analysis of boundary-layer migrants is a potentially powerful tool given the taxonomic range of insects accessible to investigators. Williams (1930), in a classic treatment, described such migrations in more than 150 butterfly species. Most of these are found in the tropics, whereas the monarch butterfly in the north temperate zone has been the target of the vast majority of investigations on insect migration (Malcolm and Zalucki 1993).

For insects, the evolution of boundary-layer migration represents a remarkable feat of goal-oriented, long-distance migration comparable to that achieved by migratory birds and bats. Using multiple sensory cues to effect directional orientation, together with monitoring of displacement and adjustment of speed according to wind conditions and net energetic expenditure, butterflies and diurnal moths fly distances ranging from hundreds to thousands of kilometers. The major unanswered questions relating to the broader purview of aerocology concern the broader implications of aerodynamics and energetics for the timing, intensity, and geographic scale of migration. Particularly useful would be studies of spatial and temporal heterogeneity in migration intensity and individual flight performance, along with simultaneous sampling across the full latitudinal transect along which these events occur.

Our research has focused on individual responses to changes in directional cues such as the sun and the Earth's magnetic field, adverse and beneficial effects of wind, and assessment of internal physiological condition such as lipid reserves. At the population level, response to changes in these states may be even more complex. Population-level analyses indicate that individuals may respond to local weather that is predictable in the short term (Srygley 2003), and to climatic conditions that are predictable in the long term (Srygley 2001b). Sexes may also differ according to their requirements for reproduction (Srygley 2001b).

We also lack a real understanding of navigation in flying insects. Goal orientation is true navigation with the use of innate vector programs or navigational maps with a directional compass and an optomotor or proprioceptive distance-meter. If an insect is capable of navigation, then it has a sense of its current position relative to a destination. For example, the remarkable migration of the monarch

butterfly from the eastern United States to its overwintering site in central Mexico probably requires that individuals alter their flight direction as they approach the overwintering site so as to increase the probability of encountering it (Schmidt-Koenig 1985). Moreover, if the insects are capable of navigation, full compensation for crosswind drift is often not the optimal strategy. For example, whereas wind drift at one location will offset drift at another, the energetic optimum may be to blow with the winds (Srygley 2003). Thus, what may appear as an inability to adjust orientation to local conditions in *U. fulgens* may be advantageous over greater distances. Analysis at both the individual and population levels will be required for a complete evaluation of optimal migration strategies. Having studied local aerodynamic, energetic, and behavioral phenomena for many years, we look forward to more decades of research on these amazing navigators.

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