

Sexual differences in tailwind drift compensation in *Phoebis sennae* butterflies (Lepidoptera: Pieridae) migrating over seas

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One prediction derived from optimal migration theory is that migrating animals that maximize their flight distance on a given amount of energy will decrease their airspeed in a tailwind and increase it in a headwind. To test this in a migrating butterfly, I followed male and female cloudless sulfur butterflies *Phoebis sennae* (Pieridae) migrating from Colombia toward Panama over the Caribbean Sea. *P. sennae* headed westerly over the Caribbean Sea in the morning and then turned southeasterly to head downwind in the afternoon. Changes in heading and track directions of *P. sennae* were not related to changes in the position of the solar azimuth. As predicted from optimal migration theory, flight velocities of females decreased in a tailwind to minimize energy consumption. However, males did not show any compensation for tailwinds. Females are minimizing energy consumption, whereas males may be minimizing the time to reach the destination site in order to maximize matings with newly arrived or newly emerged females. Orientation of females changed before that of males, presumably because their greater reproductive load imposed greater flight costs and limited flight fuels. **Keywords:** Caribbean, cloudless sulfur butterfly, drift compensation, flight, migration, orientation, *Phoebis sennae*, tropical butterflies, sexual dimorphism. [*Behav Ecol* 12:607–611 (2001)]

Theoretical analyses of the energetic costs of flight have identified optimal strategies for aerial bats, birds, and insects that migrate long distances (reviewed by Alerstam and Hedenström, 1998; Richardson, 1991). “Long distance” is obviously relative to the size of the organism, and here I apply it to distances over which a large proportion of the energy reserves of the organism are consumed.

There are four clearly defined velocities that a migrant may adopt 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 less than V_{max} and greater than V_{mr} (for recent reviews, see Alerstam and Hedenstrom, 1998; Srygley and Oliveira, 2001). The maximum range velocity is derived graphically by drawing a tangent from the origin to the U-shaped power curve for flight. However, the origin of this tangent will shift negatively with the velocity of the tailwind (and positively with a headwind; Pennycuik, 1978) such that the maximum range power is greater in a headwind and lesser in a tailwind relative to its magnitude in a still wind (Figure 1). A qualitatively similar change in airspeed with a change in tailwind is predicted for the minimum time velocity (Alerstam and Lindström, 1990). For migrating birds, adjustment of airspeed for tailwinds has been demonstrated repeatedly (see citations in Alerstam and Hedenström, 1998). Honeybees (*Apis mellifera*) reduced airspeed in a tailwind and increased airspeed in a headwind when flying 250 m across a lake (Heran and Lindauer, 1963).

Adjusting flight velocity to maximize the range that an insect is able to fly is likely to be under strong natural selection in migratory butterflies flying over the sea without access to nutrients. I investigated changes in airspeed relative to varying tailwinds in males and females of the cloudless sulfur butterfly *Phoebis sennae* migrating over the Caribbean Sea. Because I lack data necessary to generate a power curve for *P. sennae*, I based its shape on that derived for migrating moths *Urania fulgens* (Dudley and DeVries, 1990) and assumed that it is J-shaped at velocities greater than the minimum power velocity.

The use of a time-compensated sun compass or magnetic compass is also likely to be important when flying over the sea (Oliveira et al., 1998). To determine whether the orientation of the butterflies depended on the sun's position, track directions of migrating *P. sennae* were associated with the direction of the solar azimuth over the course of the day.

METHODS

Study organisms

Phoebis sennae Linn. (Lepidoptera: Pieridae: Coliadinae) is a regular migrant in the Caribbean (Brown and Heineman, 1972), Central America (Srygley RB, Oliveira EG, and Dudley R, unpublished observations) and the southeastern United States (Walker, 1991; Walker and Littell, 1994). During late November to mid-December 1997, *P. sennae* were observed migrating over the Caribbean Sea near Colombia from Cartagena to Tolú (90 km south of Cartagena; Figure 2) and as far north as Santa Marta (170 km northeast of Cartagena; Zea S and Franke R, personal communication). Butterflies were also observed flying over the Caribbean Sea 62 km southwest of Cartagena (Londono C, personal communication).

Males and females are sexually dimorphic in body size and coloration. Males are lemon-yellow and generally smaller ($n = 7$, mass = 154 ± 24 mg; $n = 6$, winglength = 35 ± 1 mm) than the off-white females ($n = 3$ females, mass = 173 ± 57 mg; $n = 2$, winglength = 37 ± 2 mm; body size data from butterflies in lowland rainforest of Panama). In Panama, lar-

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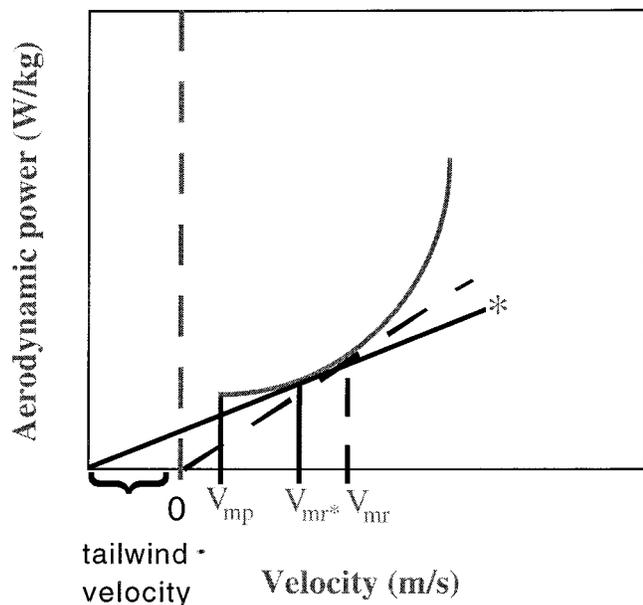


Figure 1
Theoretical construction of the hypothesized change in velocity (airspeed) for *Phoebis sennae* with a tailwind (*) relative to a still wind (after Pennycuik, 1978). The idealized power curve is adopted from that for *Urania fulgens*, a day-flying, migrating moth (Dudley and DeVries, 1990). V_{mp} is the minimum power velocity, V_{mr} is the maximum range velocity (greatest distance for the minimum energy) without wind, and V_{mr}^* is the maximum range velocity with a tailwind. See text for further explanation.

vae feed on *Senna frondosa* (formerly in the genus *Cassia*) and *Inga goldmanii* (Leguminosae; Srygley RB, unpublished data). Nitrogenous resources for spermatophore and egg production are gathered in the larval stages, and lipids are acquired during larval and adult stages (May, 1992). Both sexes gather nectar at flowers, and the adult males puddle (Srygley RB, personal observations), presumably to gather salts which are transferred to females during copulation (Pivnick and McNeil, 1987; Smedley and Eisner, 1996).

Individual butterfly airspeed, track direction, heading, and local wind

Phoebis sennae butterflies were intercepted while flying over the Caribbean Sea and followed in a 25-foot fiberglass speedboat powered by a 140-hp inboard/outboard motor until an even pace was maintained parallel to the flight direction. The pilot and I sampled butterflies flying over the water between San Bernardo Islands and Baru Island approximately 15–20 km offshore of South America on 7 and 11 December 1997, between San Bernardo Islands and Tolú approximately 10 km offshore on 8 December 1997, and approximately 15 and 10 km west (offshore) of San Bernardo Islands on 9 and 10 December 1997, respectively. Sampled butterflies remained within 0.5–8.5 m of the water surface and progressed forward steadily without evasive behavior.

Boat heading was measured with a flux-gate compass (Raytheon heading sensor M 92649) mounted on the deck, approximately 1 m above the water line. Boat speed was measured with a transducer (Airmar P55/#20-039) on a transom-mounted paddle wheel. Apparent wind direction and apparent wind speed were measured with a wind vane and anemometer (KVH Quadro network speed/wind director) mounted together on a 0.5-m aluminum pole extending over

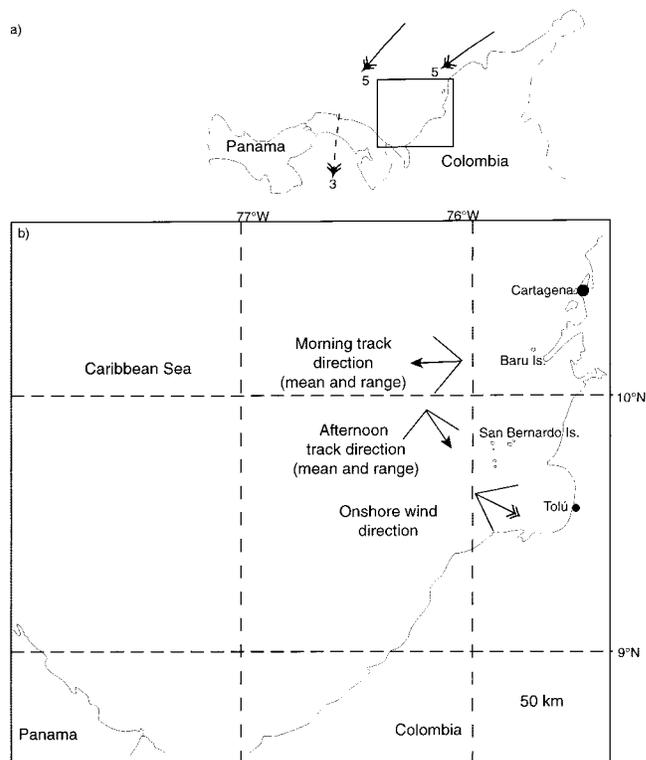


Figure 2
Maps of the study site. (a) Panama and northern Colombia with prevailing winds (double-headed arrows) in the Caribbean Sea for December (after Clarke, 1989). Numbers near the winds indicate their magnitude in the Beaufort scale (force 3 is equivalent to 3.6–5.1 m/s; force 5 to 8.7–10.8 m/s). Solid-line arrows indicate little variation in direction of winds (75% from the 90° quarter about the mean) and a constancy of 68–100%; dotted-lined arrows indicate variation in direction of winds (less than 55% in the quarter) and a velocity constancy between 45% and 68%. The square delineates the approximate area that is detailed in the map in panel (b). (b) Enlargement of the study site with mean direction and standard deviation of the winds (double-headed arrow and attached lines) over the Caribbean Sea during the study. The mean and range of track directions for *Phoebis sennae* butterflies migrating over the Caribbean Sea are divided into those observed before 1300 h and those observed after 1300 h. Locations of the arrows reflect the typical site, but not the precise location, of the measured butterflies and ambient winds.

the bow from a 2-m mast that was erected on the boat deck approximately 3–3.5 m above sea level. Data were integrated with a KVH Quadro NMEA (National Marine Electronics Association) concentrator, and true wind speed and true wind direction were calculated with a KVH Brain (4321). Positional coordinates, as well as speed and true course over ground, were collected from a deck-mounted global positioning satellite (GPS) receiver. Every 5 seconds, all data were stored in a palmtop computer (Hewlett-Packard HP200LX) with the date and time using a customized DOS BASIC program (Trimble A, unpublished application).

The navigation equipment was calibrated using standard techniques on the first morning when wind speed was 0–0.5 m/s. Across the speeds relevant to this study, mean boat speed was within 0.5 m/s of mean speed over ground (Figure 3). True wind speed was within 0.5 m/s of the wind speed measured with a Kurz hand-held anemometer when the boat was still, and error in wind direction was negligible.

While tracking a butterfly, I grouped potential landmarks

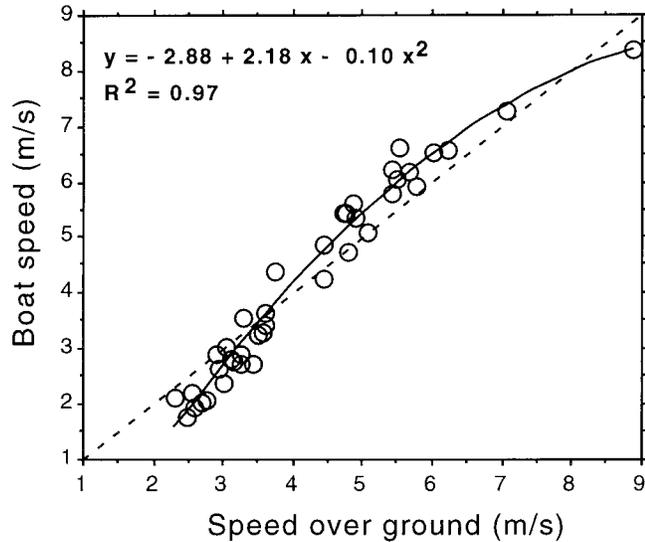


Figure 3
Calibration of the boat speed transducer with speed over ground from the global positioning system. The solid line is the polynomial regression. The dashed line indicates exact correspondence.

into three categories: none, ahead (i.e., those in the track direction), and visible (i.e., others that were not directly ahead). The insect's height over the water was estimated to the nearest 0.5 m.

I calculated the butterfly's heading and airspeed using a wind-drift vector analysis (after Srygley et al., 1996) with minor modifications for measured ground speed rather than measured airspeed. Tailwind velocity is the wind vector component along the track direction (negative for a headwind). For each individual, data were averaged for the sampled interval (butterflies were followed for 40–430 s). The female followed for the least amount of time (40 s) was lost in the glare off the sea, whereas the male followed for the least amount of time (50 s) encountered another butterfly and both circled upward until lost from view.

RESULTS

Over a similar range of tailwind velocities (Figure 4), the slopes for the regression of airspeed on tailwind were significantly different among the sexes (ANCOVA, $p = 0.011$). Airspeed declined significantly with tailwind velocity for female *P. senna* ($n = 19$, $p = .002$), whereas it was not related to tailwind velocity for males ($n = 20$, $p = 0.68$). For the males, the 95% confidence limits (CL) for the slope were -0.13 and 0.09 , of which the lower value does not eliminate a small degree of tailwind drift compensation.

Males and females were sampled at similar frequencies between morning and afternoon ($\chi^2 = 0.05$, $df = 1$, $p = .82$) and at similar frequencies with relation to the visibility and orientation of landmarks ($\chi^2 = 2.67$, $df = 2$, $p = .26$). On two dates (8 and 9 December), only males were sampled, including the two males measured in tailwinds that exceeded 4 m/s (Figure 4). The results were robust to the exclusion of males sampled on 8–9 December. The intercept for airspeed was not different from that when none of the males were excluded (4.24 m/s relative to 4.25 for all males), and the regression of airspeed on tailwind velocity was not significantly different from zero ($n = 15$, $p = .52$). Although the 95% CLs for the slope were broader due to the smaller sample size, the lower CL was less toward the predicted decline in airspeed than

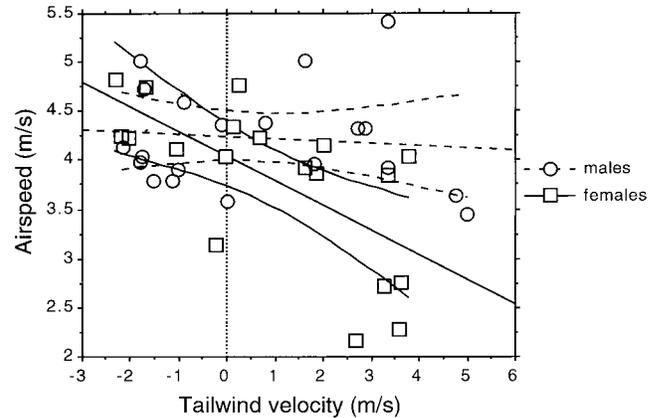


Figure 4
Linear regressions and 95% confidence limits of airspeed relative to tailwind velocity (negative values in a headwind) for male (dashed lines) and female (solid lines) *Phoebis senna*. Only the regression line for the females was significant.

when no males were excluded (-0.10 relative to -0.13 for all males). Hence, the difference between males and females in their responses to tailwind drift was not due to a difference in spatial or temporal sampling.

The sexes did not differ in flight height ($n = 17$ males, mean \pm SD: 2.7 ± 1.9 m; $n = 17$ females, 2.6 ± 2.0 m, $p = .93$). On average, males and females were followed for the same duration (mean \pm SD for $n = 20$ males: 195 ± 96 s; $n = 19$ females: 243 ± 108 s; $p = .156$), and the estimate of airspeed was not related to measurement duration ($p = .975$).

With no tailwind, the airspeed of the males (y -intercept and SE: 4.24 ± 0.12) did not differ significantly from that of the females (4.04 ± 0.16). The fact that the mean airspeeds for male and female *Phoebis senna* tended to differ ($n = 20$ males, mean airspeed \pm SE, 4.23 ± 0.12 m/s; $n = 19$ females, 3.82 ± 0.19 m/s, $p = .067$) prior to adjusting for tailwind velocity underscores the importance of analyzing airspeed data in relation to ambient winds.

Both sexes significantly shifted their headings downwind over the course of the day as wind speed increased (males, $p = .043$; females, $p = .0001$), although females did so significantly more than males (one-tailed Mann-Whitney test for angular differences: $U = 240$, $p < .05$; Zar, 1999). Furthermore, females turned downwind earlier than males (1300 h vs. 1400 h; Figure 5), although the difference is dependent on a small afternoon sample of males. Nevertheless, tailwinds increased significantly over the course of the day for females ($n = 19$, $p = .0002$), but only tended to increase for males ($n = 20$, $p = .051$). Airspeed for females also declined over the course of the day ($n = 19$, $p = .012$), but not for males ($n = 20$, $p = .478$). Apparently, the females are turning downwind, which will take them back to shore earlier than males.

On average, the butterflies track directions orient southwest ($219^\circ \pm 22^\circ$). For much of the day, track directions changed counter to the solar azimuth (Figure 6). Track directions to the south and east were frequently associated with wind speeds exceeding 3.5 m/s (Figure 6). However, some butterflies that were not flying in high winds during the afternoon also flew southeasterly toward shore (Figure 6). Hence, the butterflies' orientation changed from westerly, out to sea, in the morning to southeasterly, toward land, in the afternoon, resulting in a southwesterly progressing, zigzagged route along the Atlantic coast of Colombia.

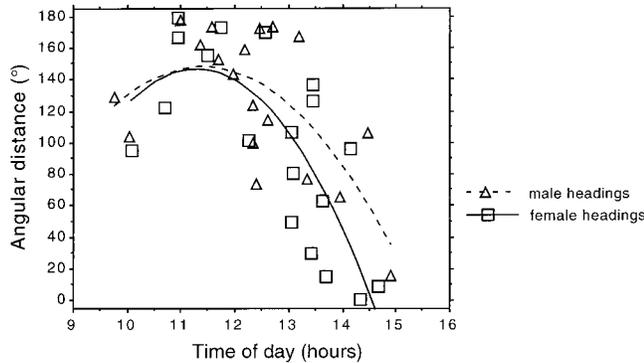


Figure 5
Change in the angular difference between headings of *Phoebis sennae* flying over the Caribbean Sea and the ambient wind direction over the course of the day. The two curvilinear lines represent the polynomial regression for male (dashed line) and female (solid line) headings. At zero, heading and wind are in the same direction.

DISCUSSION

The southwesterly track direction of the migrating cloudless sulfur *Phoebis sennae* is directed toward the wet Atlantic forest of Darien, Panama, where they may spend the dry season in shadier, more humid conditions (ca. 180 km from the dry forest near Cartagena, Colombia; Figure 2). If the behavior of each individual that is sampled at a specific time indicates the behavior of the population over the course of the day, then a reasonable picture of the migration emerges. For those butterflies that are able to fly west far enough from shore, the strength and southwesterly direction of the trade wind prevalent offshore at this time of year (9–11 m/s; Clarke 1989) may facilitate arrival at the presumed destination site (a butterfly's ground speed would be ca. 50 km/h). However, for butterflies that leave the coast too late or otherwise fail to reach the region where trade winds predominate offshore, southeasterly onshore winds increase in strength during the afternoon and drift them toward coastal Colombia. These butterflies turn downwind toward a coastal site that is nearer to Panama than the site at which they departed the coast, and presumably continue to migrate southwesterly toward Panama on subsequent days (see also Srygley, 2001).

In a tailwind, female *P. sennae* reduced their airspeeds, whereas males did not. To the best of my knowledge, a difference among the sexes in tailwind drift compensation has not been reported in insects. Females may have reduced their velocity to a speed that maximizes range in the tailwind (Pennycuik, 1978), such that they minimize the consumption of lipids that would otherwise be allocated to eggs and can safely reach the shore. In contrast, males may be selected to minimize their flight time to the destination site by adopting a maximum sustainable velocity. The males probably adopt V_{\max} rather than V_{mt} because the flight is over water where there are no stopover sites to replenish energetic resources.

By adopting a maximum sustainable velocity, a male's early arrival at the breeding site may result in an increase in the number of copulations relative to males that arrive later (also see Myers, 1981). Protandry, or the early emergence and entrance to the population by adult males, occurs in a number of butterfly species (Nylin et al., 1993; Wiklund and Fagerström, 1977), and it is strongly selected for in populations with discrete generations (Singer, 1982). I suggest that early arrival to suitable habitats by adult male butterflies is also selected for in seasonally migrating populations.

It is reasonable to assume that female *Phoebis sennae* are

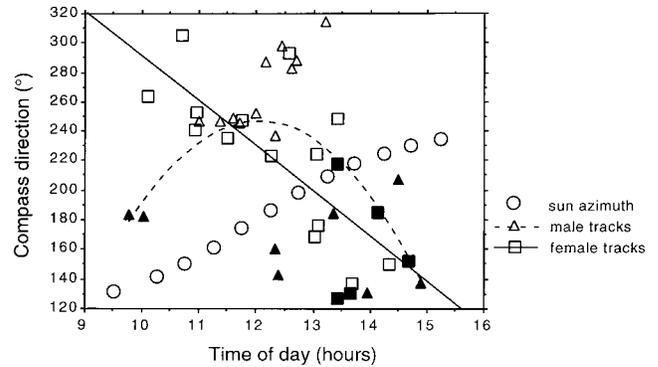


Figure 6
Change in track directions of *Phoebis sennae* flying over the Caribbean Sea relative to change in the position of the solar azimuth over the course of the day. The dashed line represents the polynomial regression for males, and the solid line represents the least-squares regression for females. Neither line is associated with the change in the position of the solar azimuth. Filled symbols identify butterfly directions when wind speeds exceeded 3.5 m/s.

sexually immature; in other words, they exhibit the oogenesis flight syndrome typical of other migrating insects (Johnson, 1969; Rankin and Burchsted, 1992). In Florida, the majority of migrating female *P. sennae* were unmated (Walker, 1978). The steady immigration or local emergence of virgin females would increase the mating success of early- relative to late-arriving males. There may also be selection for males to emerge and migrate earlier than females, although early migrants may lose safety in numbers that results from migrating en masse. Nevertheless, flight speeds near V_{\max} would result in the male's arrival ahead of other males and of females in its consort that began migrating on the same day. The greater energetic cost of flying at V_{\max} serves as a counterselective force.

Liechti et al. (1994) developed a model for wind compensation that incorporates both crosswinds and tailwinds. However, the model depends on compensation for crosswind drift, at least in part. Four of 17 *Phoebis sennae* tested compensated for crosswind drift over the Caribbean Sea (Srygley, 2001). Therefore, it is not possible to test a more complex model optimizing compensation for crosswind and tailwind drift simultaneously with this data set.

To gauge the speed of a tailwind when flying over the sea, butterflies may use the sea surface as a ground reference. The accuracy of this method is compromised because the sea surface also moves in the direction of the wind, although not as quickly. A butterfly might also turn upwind and fly at a speed that holds landmarks on the horizon stationary, thus gauging the windspeed against its own airspeed. In this study, a landmark-based method would not have been possible in the 21 cases for which none was visible. Butterflies are occasionally, but rarely, observed circling when over water, which might provide useful information on ambient winds. However, behaviors that might provide insight into how butterflies gauge wind speed were not consistent.

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REFERENCES

- Alerstam T, Hedenström A, 1998. The development of bird migration theory. *J Avian Biol* 29:343–369.
- Alerstam T, Lindström A, 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: *Bird migration: the physiology and ecophysiology* (Gwinner B, ed). Berlin: Springer; 331–351.
- Brown FM, Heineman B, 1972. Jamaica and its butterflies. New York: E.W. Classey.
- Clarke J, 1989. Atlantic pilot atlas. London: Stanford Maritime.
- Dudley R, DeVries PJ, 1990. Flight physiology of migrating *Urania fulgens* (Uraniidae) moths: kinematics and aerodynamics of natural free flight. *J Comp Physiol A* 167:145–154.
- Heran H, Lindauer M, 1963. Windkompensation und Seitenwindkorrektur der Bienen beim Flug über Wasser. *Z vergl Physiol* 47:39–55.
- Johnson CG, 1969. Migration and dispersal of insects by flight. London: Methuen.
- Liechti F, Hedenström A, Alerstam T, 1994. Effects of sidewinds on optimal flight speed of birds. *J Theor Biol* 170:219–225.
- May PG, 1992. Flower selection and the dynamics of lipid reserves in two nectarivorous butterflies. *Ecology* 73:2181–2191.
- Myers JP, 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can J Zool* 59:1527–1534.
- Nylin S, Wiklund C, Wickman P-O, Garcia-Barros E, 1993. Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. *Ecology* 74:1414–1427.
- Oliveira EG, Srygley RB, Dudley R, 1998. Do Neotropical migrant butterflies navigate using a solar compass? *J Exp Biol* 201:3317–3331.
- Pennycuik CJ, 1978. Fifteen testable predictions about bird flight. *Oikos* 30:165–176.
- Pivnick KA, McNeil JN, 1987. Puddling in butterflies: sodium affects reproductive success in *Thymelicus lineola*. *Phys Entomol* 12:461–472.
- Rankin MA, Burchsted JCA, 1992. The cost of migration in insects. *Annu Rev Entomol* 37:533–559.
- Richardson WJ, 1991. Wind and orientation of migrating birds: a review. In: *Orientation in birds* (Berthold P, ed). Basel: Birkhäuser Verlag; 226–249.
- Singer MC, 1982. Sexual selection for small size in male butterflies. *Am Nat* 119:440–443.
- Smedley SR, Eisner T, 1996. Sodium: a male moth's gift to its offspring. *Proc Natl Acad Sci USA* 93:809–813.
- Srygley RB, 2001. Compensation for fluctuations in crosswind drift without stationary landmarks in butterflies migrating over seas. *Anim Behav* 69:191–203.
- Srygley RB, Oliveira EG, 2001. Migration patterns and orientation mechanisms within the flight boundary layer. In: *Insect movement: mechanisms and consequences* (Reynolds D, Thomas C, Woiwod I, eds). London: CAB International; 183–206.
- Srygley RB, Oliveira EG, Dudley R, 1996. Wind drift compensation, flyways, and conservation of diurnal, migrant neotropical Lepidoptera. *Proc R Soc Lond B* 263:1351–1357.
- Walker TJ, 1978. Migration and re-migration of butterflies through north peninsular Florida: quantification with Malaise traps. *J Lepidopt Soc* 32:178–190.
- Walker TJ, 1991. Butterfly migration from and to peninsular Florida. *Ecol Entomol* 16:241–252.
- Walker TJ, Littell RC, 1994. Orientation of fall-migrating butterflies in North peninsular Florida and source areas. *Ethology* 98:60–84.
- Wiklund C, Fagerström T, 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* 31:153–158.
- Zar JH, 1999. *Biostatistical analysis*. Upper Saddle River, New Jersey: Prentice Hall.