Sun compass and wind drift compensation in migrating butterflies

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Abstract: Migrating pierid butterflies use a sun compass in order to head in a preferred flight direction. When blown off-course by the wind, butterflies adjust their heading to compensate for cross-track wind drift. They are capable of drift compensation over water when and where landmarks are visible on the shore. They are also capable of a more inaccurate form of drift compensation over the sea when and where landmarks are not visible.

Introduction.

Despite the economic importance of migrating insects, we know relatively little about their abilities to orient and navigate. For migrating butterflies, three non-mutually exclusive hypotheses have been put forward to explain their abilities to orient and navigate: use of landmarks, orientation with a sun compass, and use of a geomagnetic compass (Brower 1996). In Panama, we have focused on migrating butterflies in two families (Lepidoptera: Pieridae; Nymphalidae), a diurnal moth in the family Uraniidae, and two species of dragonflies (Odonata: Libellulidae). Because the sulphur butterflies in the genera Aphrissa and Phoebis are abundant, we have done most of the research on navigation and orientation mechanisms in these butterflies. In this paper, we will briefly summarize mechanisms for orientation and navigation from our research drawing upon the literature for comparisons with other species.

General methodology. In order to characterize annual variation in numbers of butterflies migrating, and the extent of the migrations, we have measured and counted the number of butterflies flying in each compass direction at a number of locations spanning the isthmus of Panama. We have focused on the mass migration period between May-July of each year for the past decade. However, in order to understand more fully the association of the migration phenology with variation in environment and resource availability, we have also measured flight directions throughout the year during September 1994-October 1998. On land, we measure vanishing bearings of migrating butterflies at various locations across the isthmus of Panama and the Colombian coast. We also have erected ‘malaise-style’ traps at various localities which sample butterflies flying in two directions, one with the general migratory flow and the other contrary to it.

We have also taken advantage of the fact that long-distance migrating insects fly across large bodies of water to investigate the use of a sun compass and local landmarks as orientation cues. Pacing insects with a motorized boat (a method first developed by DeVries and Dudley 1990, Dudley and DeVries 1991 for following migrating Urania moths) permits us to measure ground velocity and track direction while simultaneously measuring wind speed and direction (a refined method developed by Srygley 2001a,b). As a result, we are able to estimate the insect’s airspeed and heading and measure changes in airspeed and heading within individuals as environmental conditions vary and among individuals as both environmental and internal conditions vary.

Simultaneous measurements of wind speed, wind direction, ground speed, and track direction was accomplished with commercially-available, sailboat navigation equipment (Srygley 2001a,b). Boat heading was measured with a flux-gate compass (Raytheon heading sensor M92649) mounted on the boat 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 aluminium pole extending over the bow from a 2 m mast that was erected on the boat deck approximately 3-3.5 m above sea level. Boat speed, boat heading, apparent wind speed and apparent wind heading were integrated with a KVH Quadro NMEA (National Marine Electronics Association) concentrator, and wind speed and wind direction were calculated with a KVH Brain (4321). The NMEA output was transmitted to a palmtop computer (Hewlett-Packard HP200LX), in which it was read, converted into ASCII character text, and electronically stored with the date and time every 5 s using a customised DOS BASIC program (see Srygley 2001 a,b for calibrations).

The evolution of directional migration. The fitness of long-distance migrants is dependent on the suitability of the habitat in which the migrants finally place their gametes. We presume that there is variation in the suitability of destinations for reproduction such that movement is more favourable for reproduction than at the origin (Figure 1a). In fact, fitness at the destination must, on average, exceed the

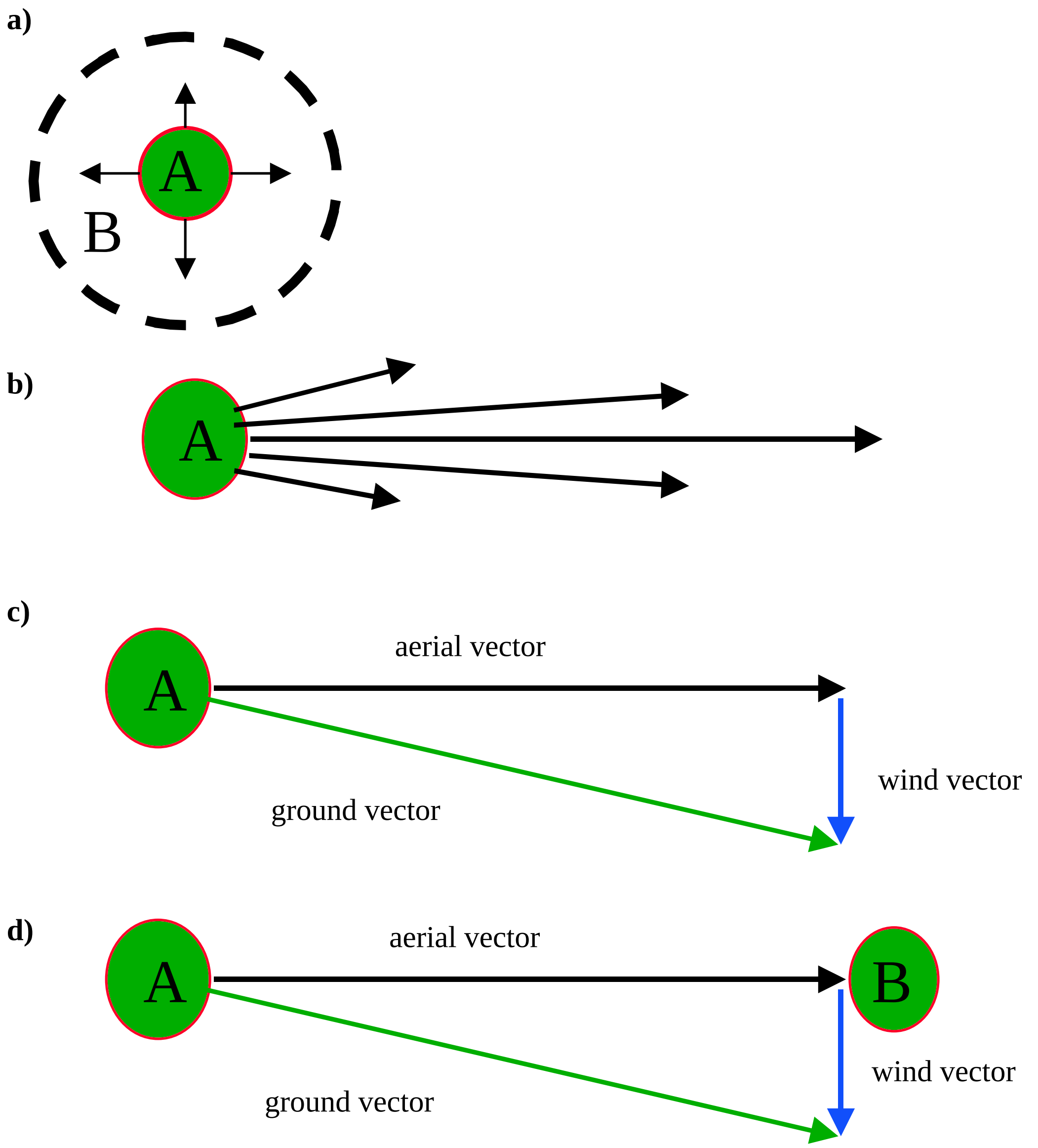


Figure 1. Four phases in the evolution of long-distance migrations. a) Dispersal from A to B. Fitness in region B exceeds, on average, fitness in Region A, plus loss of fitness due to dispersal. B) Dispersal becomes more constrained in direction when fitness varies with direction about a mean ‘preferred’ direction. Insects may use environmental gradients in temperature, humidity, air pressure, etc. as directional cues. The length of the arrow indicates the number of individuals adopting a particular flight direction following selection. C) To assure maintenance of direction in a fluctuating environment, migrating insects may adopt an endogenous compass and the use of local cues to adjust heading for wind drift. D) A destination site evolves when fitness varies with both direction and distance travelled.

combined cost of unrealized fitness at the origin plus unrealized fitness including increased risk of mortality during dispersal (see also Baker 1984).

Secondly, for directionally oriented migrations to arise, we presume that there is variation in the suitability of destinations for reproduction such that selection is operating on a genetic mechanism that orients the insect in a ‘preferred’ direction of dispersal (Figure 1b). Directional cues may come from prevalent winds, or environmental gradients in temperature, humidity, or air pressure.

Given the importance of directional orientation that we have ascribed to it, we might then expect that butterflies evolve an endogenous compass to orient in a ‘preferred’ direction over long distances. Furthermore, selection varies depending on the fitness gained from reaching suitable destination sites. Therefore mechanisms to maintain course when winds are unfavorable may also have a heritable component and evolve in response to natural selection (Figure 1c).

Finally, variation in the suitability of destinations with distance must also influence selection on distance or duration travelled (Figure 1d). For example, mating opportunities are likely to be more common where the majority of co-migrants settle. As a result, selection for travelling a particular distance in a particular direction leads to the origin of a destination site.

Orientation of the migrants in Panama and over the Caribbean Sea.

We have mapped the flyway for pierid butterflies migrating over the Caribbean Sea and across the isthmus of Panama (Figure 2). Complete sampling of the migration tracks for all species is hindered by logistical difficulties. The flyways cover an area from 100 to 500 km in length, and much of the land is accessible only by foot and the sea only by boat.

Aphrissa statira (Cramer) butterflies migrate en masse across the isthmus of Panama in May-July of each year (see Oliveira et al. 1998 for among year variation in numbers). In a boat, we followed butterflies as they flew individually south by southwest over the Caribbean Sea heading toward a point of land that projects toward the islands of San Blas. This ‘stream’ of butterflies was apparently very narrow, because we sampled a two kilometer transect along the Atlantic coast on either side of the point, and the number of butterflies quickly dropped off within a few hundred meters to either side. Once on shore, the coastal mountain range may hinder their movement directly across the isthmus. Because the mean flight direction of A. statira at Portobelo was significantly different from other locations along the flyway, we hypothesize that the butterflies fly more westerly along the coast. At Portobelo, the elevation of the isthmus declines dramatically to near sea level. Within a few kilometers, A. statira once again adopt a south by southwest track (approximately

Figure 2. Mean flight directions for Aphrissa statira in May-June are designated by arrows drawn from census sites on the isthmus of Panama. The arrow at Cartagena, Colombia is the mean flight direction of Phoebis sennae butterflies in December 1997. Over the Caribbean Sea, the mean flight direction of P. sennae changed from westerly out to sea in the morning to south-easterly toward the Colombian coast in the afternoon. The mean flight direction is depicted as the third arrow head between these two directional arrows. See the text for further details.

205°) that is maintained in a narrow band across the isthmus of Panama (Srygley et al. 1996). We also measured A. statira departing Colombia at Baru Island near Cartagena in June 1996. However, no butterflies were observed departing Colombia the following year, eventhough there was a large scale migration observed crossing the isthmus of Panama at that time. From these observations, we hypothesize that the Colombian population might contribute to but is not essential for a migration of the Panamian population.

For Phoebis argante (Fabricius), we have fewer samples of sites along the putative flyway. However mass migration does occur each year across the Panama Canal near Barro Colorado Island (BCI) during the same months and in approximately the same direction as A. statira (e.g., Figure 2 in Oliveira et al. 1998).

A large scale migration of Phoebis sennae (L.) butterflies was sampled off the Caribbean coast of Colombia during December 1997 (Srygley 2001a,b). Although the mean flight direction of the migrants was the same south by southwest direction as that across the isthmus of Panama in May-July, flight directions changed systematically over the course of the day. Butterflies flew westerly out to sea in the morning and then turned to fly in a more southerly direction in the afternoon. As a result, the track zigzags west and then south again down the coast of Colombia. We hypothesize that the butterflies are flying west toward the prevalent northeasterly trade winds that will carry them to the Atlantic coast of Panama. Hence, only those butterflies that fail to reach the trade winds offshore change direction due to their failure to overcome the strengthening northwesterly onshore winds in the afternoon (Figure 2: the triple arrow over the Caribbean Sea depicts the westerly, morning and southeasterly, afternoon flight directions with the mean flight directions for all butterflies between them).

Thus far, the directional orientation of these three pierid butterfly species is consistent with the second phase of our evolutionary scenario. Butterflies adopt a ‘preferred’ flight direction. Across the isthmus of Panama, an environmental gradient in humidity spans from the lowland wet forests of the Atlantic coast to the dry forests of the Pacific coast. This environmental gradient is a result of the winds that prevail from the north to northwest on the isthmus of Panama in May-July, and from the northeast over the Caribbean Sea near to Colombia. More sophisticated than adopting a single, invariant flight direction, the ‘preferred’ flight direction of Aphrissa statira changes with location and that for Phoebis sennae changes with time of day.

Sun compass. How does each individual fly toward a ‘preferred’ flight orientation? For Aphrisssa statira and Phoebis argante, we have demonstrated use of a time-compensated sun compass, which may be used for orienting over long distances

(Oliveira et al. 1996, 1998). Orientation is manifested by directing the body at a particular angle relative to the sun's azimuth. An endogenous clock corrects for the change in the sun's azimuth over the course of the day.

The mechanism by which time-compensation is achieved and the degree of compensation may vary among species. Full compensation requires innate or learned information about the position of the solar azimuth over the course of the day. This ephemeris function is specific to the time of year and latitudinal position on the Earth. Alternatively, the insect might approximate the position of the solar azimuth with a time-averaging function. For example, a migrant might approximate the change in the sun's position as 15° per hour. Such a rule would have its greatest errors at mid-morning and mid-afternoon. A third potential mechanism is to evolve a step-function to approximate the change in the solar azimuth. For example, a rule that the azimuth is in the east in the morning (90°) and the west in the afternoon (180°) would have its greatest error at mid-day (Srygley and Oliveira 2001).

In Panama, Aphrissa statira butterflies were captured while migrating across a lake and separated into two groups. The experimental group was placed in an environmental chamber in which the light regime was shifted 4-hours in advance of natural time. The control butterflies were handled identically, but the light regime in their environmental chamber was near to that of natural time. The predicted result depended on the time-compensation mechanism adopted. The butterflies would shift 120° under the full-compensation hypothesis, 60° under the time-averaging hypothesis, and 180° under the step-function hypothesis. Experimental A. statira butterflies (n=91) shifted their headings 91° on average relative to the control butterflies (n=97). Ninety-five percent confidence limits (56°, 126°) excluded the step-function hypothesis, but they did not distinguish between the full-compensation and time-averaging hypotheses (Oliveira et al. 1998).

Under the same experimental regime, P. argante butterflies shifted their headings 83° on average(Oliveira et al. 1998). The sample size was much smaller (n=19 experimental and n=17 control P. argante), but the 95% confidence limits (5°, 161°) excluded the step-function hypothesis. Once again, we were unable to distinguish between the full compensation and time-averaging hypotheses.

In a third recent clock-shift experiment, Perez et al. (1997) delayed the biological clocks of autumnally migrating monarch butterflies (Danaus plexippus L.) by six hours in Kansas, USA. The authors concluded that the resulting heading of experimental butterflies was 287°±46° (n=43, mean ± 95% confidence intervals, confidence intervals were calculated from published r=0.29). By contrast, the mean heading of control butterflies was 211°±22° (r=0.67), a value similar to that for naturally flying migrants (200°). In Kansas, assuming an afternoon release, Danaus was predicted to shift approximately 120° with full-compensation, 90° with time-averaging compensation, and 180° with step-function compensation. The insects shifted 76°±68° relative to sham controls, excluding the step-function hypothesis (Note: the 95% confidence intervals were estimated by adding together the 95% C.I. for the mean experimental and control directions). From this published study, we were unable to distinguish between full compensation and time-averaging in monarch butterflies.

Use of landmarks. The long distance migrants use a sun compass to orient their heading over large distances. Over short distances, butterflies modify their flight orientation with landmarks. We have observed Aphrissa statira butterflies flying over the Caribbean Sea toward a peninsula (Figure 2), suggesting that butterflies are able to detect and use landmarks from at least 200 meters. The distance between butterflies was too great for one to follow another, and the alternative hypothesis of an endogenous compass pointing directly to that terrestrial landmark seems unlikely.

Correction of flight paths for crosswind drift when the butterflies are flying over water provides additional evidence for the use of landmarks. The Florida white, Ascia monuste flew in a curvilinear track between islands off the Florida coast, indicating its use of a single landmark (Nielsen 1961). The sulphurs Aphrissa statira adjusted their headings to correct for crosswind drift when crossing a lake that was approximately 1.5 km wide (Srygley et al. 1996). Their ability to maintain a straight track when drift varied indicated that they did not use a single landmark to correct for drift (figure 3). The data were consistent with either of two other mechanisms: use of two landmarks in parallax which would result in full compensation for crosswind drift (regression slope = 0), or use of the surface of the water as a ground reference ($0<$ slope <1). Overcompensation would result in a slope less than zero. The downwind motion of the water would result in partial compensation for crosswind drift (Srygley and Oliveira 2001).

Over the Caribbean Sea, Phoebis sennae butterflies tended to not compensate for the mild winds in the morning when only the sea and clear sky were visible, and overcompensate for the strong winds in the afternoon when land and clouds were visible (Figure 4, Srygley 2001a). The landmarks (e.g., the coastline) were generally to one side of the direction that the butterfly was flying. Landmarks may be used over long distances to maintain the flight path at the same distance from the coast. The observed prevalence of overcompensation in the afternoon may reflect a change in flight direction upwind and down the coast to overcompensate for the strong onshore winds that bring the butterflies closer to shore.

Figure 3. Change in track direction versus change in wind drift for individual A. statira butterflies as they crossed Lake Gatun, Panama. The slope for no compensation is predicted to be 1.0, and the slope for full compensation is predicted to be 0.0. A slope between 0.0 and 1.0 would indicate part compensation. From the data, we were able to reject the null hypothesis of no compensation.

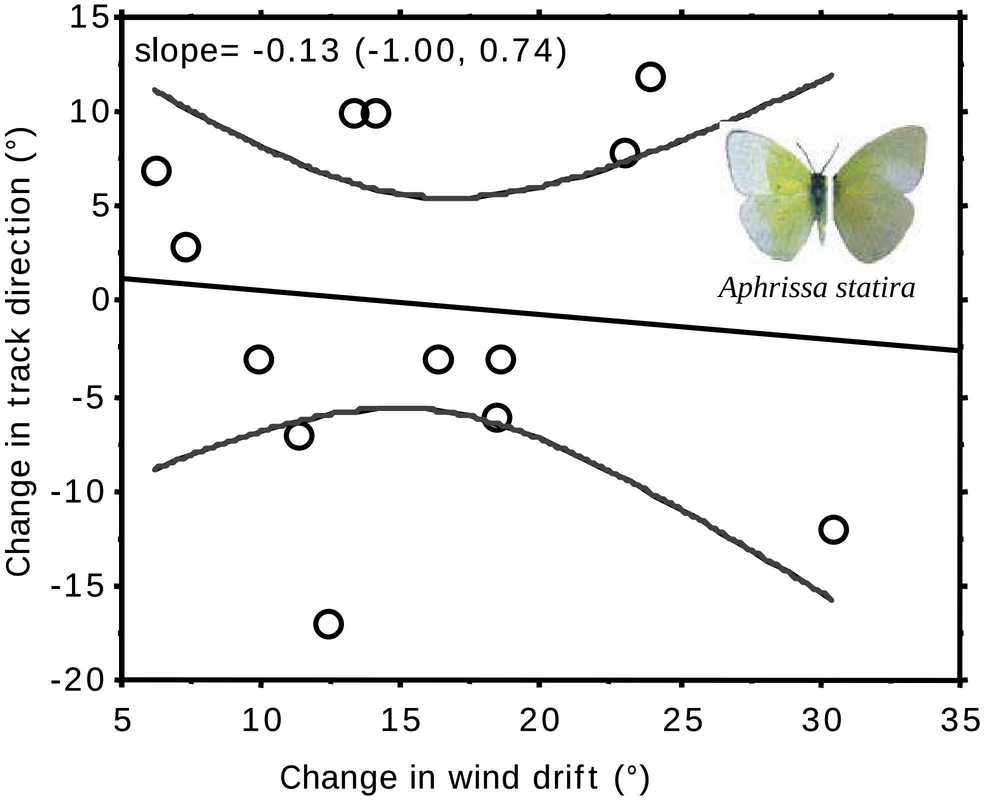
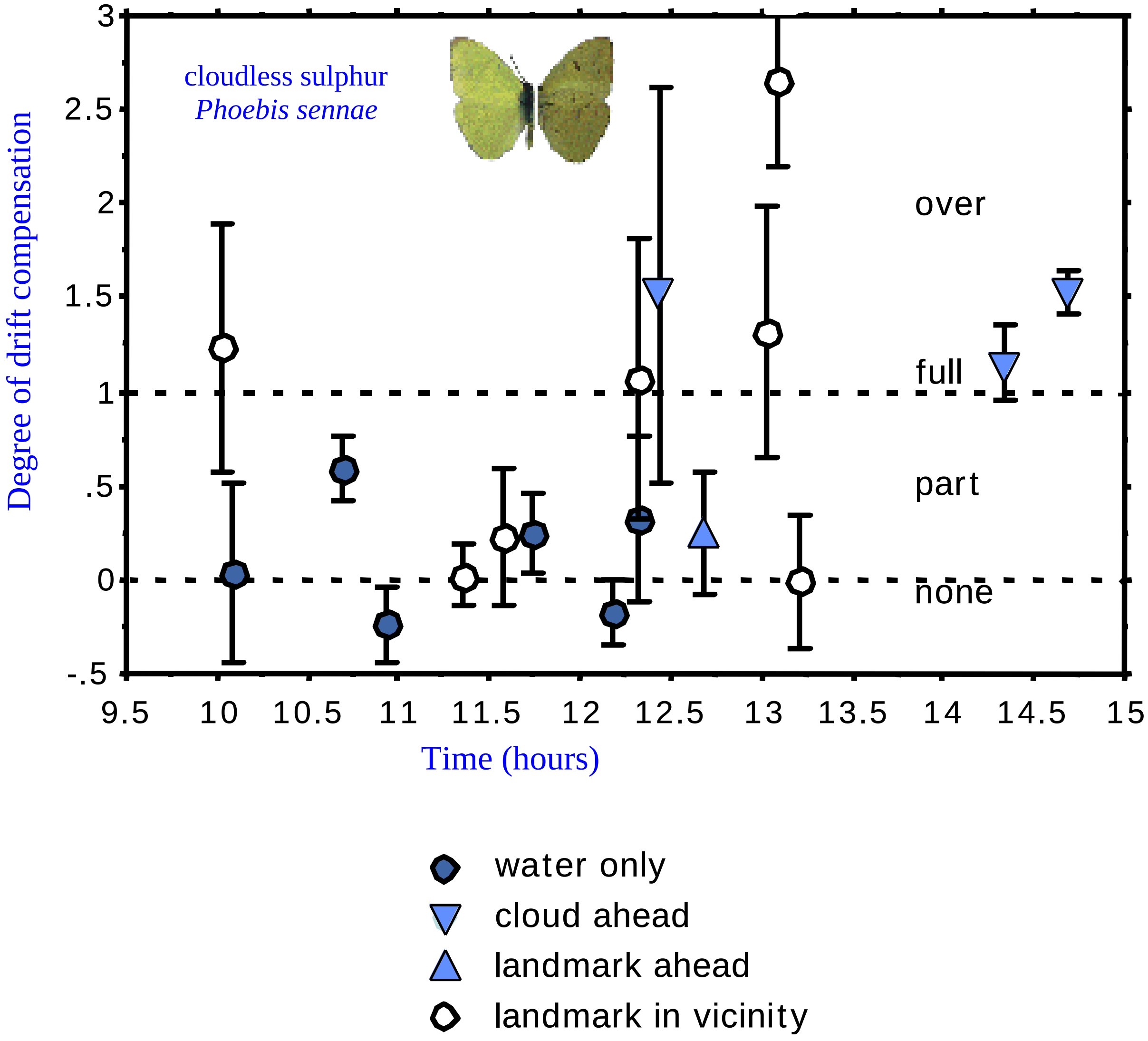


Figure 4. Degree of drift compensation with and without terrestrial or celestial landmarks in Phoebis sennae butterflies flying over the Caribbean Sea. Butterflies were more likely to compensate for crosswind drift when landmarks were visible, but they were capable of full or over compensation when only clouds were present.



A much more likely cue to correct for wind drift in the open sea is the sea surface used as a ground reference. Partial compensation for wind drift is the predicted result if the butterflies use the sea surface, and partial compensation was observed in the only butterfly flying over the open sea without celestial cues other than the sun and without terrestrial cues other than the sea surface.

Now that we know the butterflies orient with a sun compass and maintain course when drifted by the wind, we conclude that Aphrissa statira and Phoebis sennae are consistent with the fourth phase of our evolutionary scenario. Butterflies adopt a ‘preferred’ flight direction and use a time-compensated sun compass. The adopted heading results in a corresponding track direction when there is no crosswind. More typically butterflies are displaced from their preferred course by a crosswind. Then the butterflies adjust their headings to compensate for the wind drift. The degree of compensation is dependent on the strength of the wind and presence of landmarks. When winds were light, butterflies were more likely to compensate fully over a lake where landmarks were present. Over the Caribbean Sea the position of landmarks relative to the flight path made them unfavorable as a cue for correcting course. As a result, the degree of compensation was imprecise and the butterflies tended to overcompensate for crosswind drift. As a result of overcompensation, the migrants had a track that zig-zagged along the coast of Colombia toward Panama.

Magnetic compass. As with the sun, the Earth’s magnetic field may also provide orientation information for some insects that navigate long distances. Thus far, a magnetic sense in butterflies has not been demonstrated. Perez et al. (1999) approached autumnally migrating monarch butterflies with a magnet prior to release, and the headings of magnetised butterflies were random whereas that of control butterflies were directed to the Southwest. However, the evidence was weakened by the fact that the experimental butterflies’ mean track direction (328°, including effects of the wind) was not different from that of the control group (326°). Butterflies compensate for wind drift by changing their headings (Srygley et al. 1996), and wind drift may have been different at the times of release of butterflies in the two groups. In addition, both mean track directions were toward the Northwest, whereas vanishing bearings of naturally migrating butterflies were toward the South (194°). More recently, Etheredge et al. (1999) reversed the orientation of autumnally migrating monarchs inside an indoor arena within which the Earth’s magnetic field was locally reversed using a Helmholtz coil, but these impressive results were later withdrawn due to experimental bias (Etheredge et al. 2000).

Spieth and Kaschuba-Holtgrave (1996) have recently developed an experimental set up to study migratory orientation of European Pieris brassicae which for the first time enabled flight orientation of naturally migrating butterflies to be reproduced in circular cages. If this method is applicable to other species, it may prove useful for investigating environmental, genetic, and developmental factors that influence orientation behaviour of migrating insects (see also Spieth and Kaschuba-Holtgrave 1996; Spieth et al., 1998). Moreover, carefully controlled experiments could begin to tease apart the migrant's ability to evaluate and integrate directional information derived from the sun, polarized skylight, local landmarks, wind speed and direction, and geomagnetism.

Navigation.

Much of the theoretical research on bird migrations has not crossed over into insects. In part, this is due to our lack of understanding of the insects' abilities to orient and navigate, which imposes constraints on assumptions of the models. True navigation requires the animal has a sense of its current position relative to a destination site. This may be innate, as in a vector program of directions and distances to be travelled, or learned as a cognitive map. For example, the autumnal

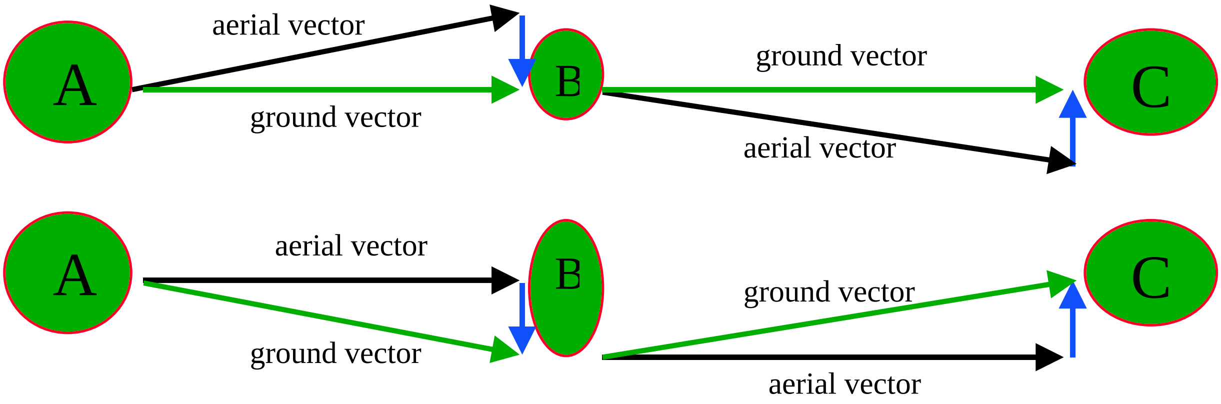


Figure 5. a) If the insects are unable to navigate but fly oriented in a preferred compass direction, optimality models lead to the same predictions for minimizing flight duration and energy consumption. However, risk of drift away from suitable destination areas increases because of an inability to navigate. Hence, full compensation is probably the most successful strategy. B) If the insect is able to navigate, then full compensation is often not the optimal strategy. For example, when wind drift varies predictably both spatially and temporally as depicted, the energetic optimum would be to not compensate for wind drift on either segment of the migration.

migrating monarch butterflies fly from their origins to an overwintering site in central Mexico. It is probable that individual butterflies alter their flight direction as they migrate so that they increase the probability of encountering the destination site (e.g., Schmidt-Koenig 1985).

True navigation gives rise to the possibility of elaborate mechanisms of drift optimization (Alerstam 1979). Full compensation minimizes flight duration and energy consumption relative to partial or no compensation when wind conditions are constant during the migration. However, when wind direction changes in a predictable manner (Figure 5), no compensation for wind drift may be energetically less costly than full compensation. When wind conditions vary, an increase in the degree of compensation (i.e., flexible compensation from none to partial to full) as the migrant approaches its destination minimizes flight duration and energy consumption.

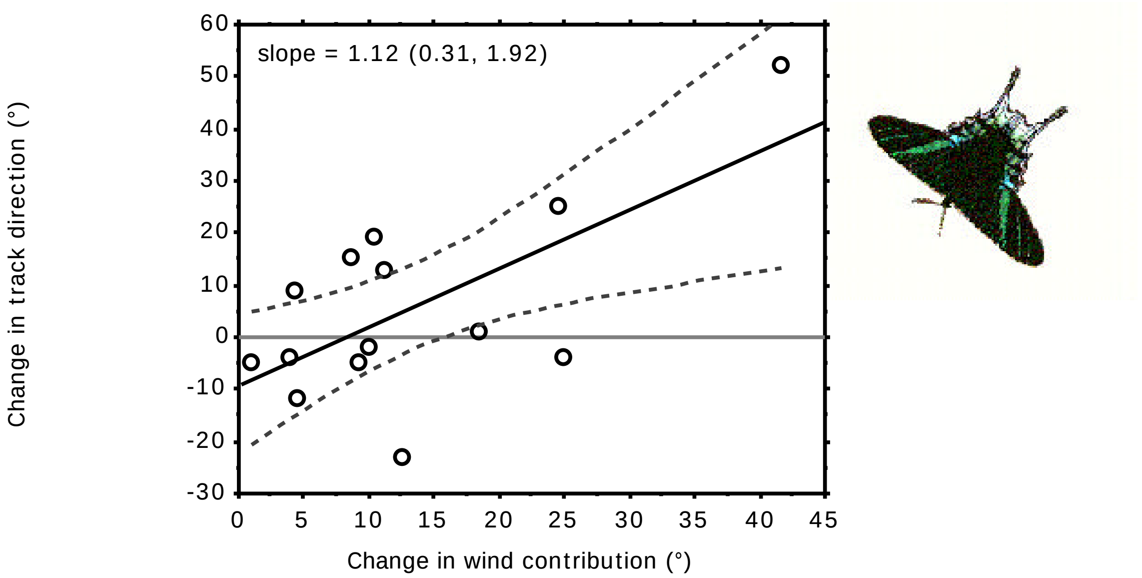


Figure 6. Change in track direction versus change in wind drift for individual Urania moths as they migrated across Lake Gatun, Panama. We were unable to reject the null hypothesis of no compensation, but the insects may have been compensating in part.

Urania fulgens, a diurnally migrating moth, did not compensate significantly for wind drift when crossing Lake Gatun in the Panama Canal (Figure 6). However, to conclude that it is incapable of drift compensation based on its behavior at a single site may be erroneous. A tactic of drifting with the wind may minimize energy consumption should drift be compensated with less energetic cost at another point in the track.

Changes in orientation over a large spatial scale may be indicative of navigating towards a goal. Aphrissa statira butterflies fly along the Atlantic coast of Panama, and then alter their flight directions to head southwest into the interior crossing the isthmus in the region of the Panama Canal.

An alternative hypothesis is that a conflict between topography and the preferred flight direction of the butterfly results in a change in flight orientation. For example, changes in topography that are readily visible probably result in concentrations of insects at mountain passes (Beebe 1949, 1951; Beebe and Fleming 1951) and concentrations of butterflies departing points of land at land-water interfaces (RBS and EGO, personal observations). Presumably the insects alter their flight direction to avoid adverse situations. We propose a risk-secure direction is adopted when it does not conflict greatly with the ‘preferred’ orientation (Figure 7). The degree to which a risk secure direction may diverge from the ‘preferred’ direction will depend on the cost incurred by altering course relative to the benefits accrued from the reduction in risk to fitness (as a result of injury, mortality, or settlement in a less ideal site relative to the destination site).

Thus, at the Atlantic coast of Panama, Aphrissa statira may turn toward the west to avoid the risk-prone mountains. The difference in direction is approximately 75° relative to the ‘preferred’ orientation of 205° at the other sites. Once the butterflies reach the pass through the mountains at the region of the Panama Canal, then they adopt the ‘preferred’ direction.

Over the Caribbean Sea, Phoebis sennae butterflies flew west away from the Colombian coast in the morning and changed direction to fly south in the afternoon. We speculate that this represents an innate program to fly towards the predictably strong trade winds that occur offshore. If the trade winds are not reached, the strong afternoon onshore winds drift the insects towards the shore. In the afternoon, the butterflies adopt a more southerly direction that maximizes their distance flown toward the putative destination site in Panama.

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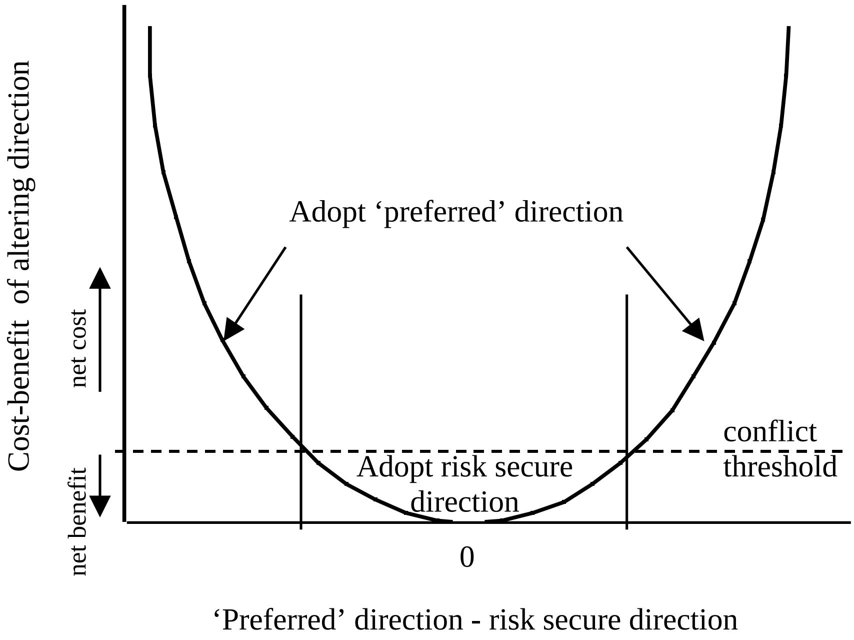

Figure 7. A model of altering direction from the endogenous, 'preferred' direction when confronted with a risk of reduction in fitness. The difference is 0 when the most risk secure direction is the same as the preferred direction. With greater change in direction from the 'preferred' compass direction, the cost of recovering the distance or time lost increases on either side of 0. Organisms should adopt the preferred direction when the cost is too great to warrant the change in direction.

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