

## **Wind Drift Compensation in Migrating Dragonflies *Pantala* (Odonata: Libellulidae)**

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*Tailwind drift compensation serves to maximize a migrant's flight distance on a given amount of energy, and crosswind drift compensation serves to hold a course true and minimize the distance flown. With full or part compensation, airspeeds are predicted to increase with greater crosswind drift. To test whether migrating dragonflies compensated for wind drift, I measured the velocity and heading of *Pantala hymenaea* and *P. flavescens* in natural flight over a lake and the ambient wind speed and direction. *P. hymenaea* flew northeasterly (58°), whereas *P. flavescens* flew significantly more east–north easterly (74°) throughout the day. *Pantala* spp. demonstrated part compensation for changes in crosswind drift within individuals (mean compensation = 54%,  $P = 0.0000$ ), evidence for use of a ground reference to correct for drift when flying over water. Among individuals, *P. flavescens* compensated for crosswind drift. *P. hymenaea* overcompensated and then drifted downwind on one morning and compensated for crosswind drift on the next. As predicted from optimal migration theory, airspeed (5.0 m/s for both species with no tailwind) decreased with tailwind velocity both among individuals (data for both species pooled [ $n = 19$ ],  $P < 0.0001$ ) and within each individual as it crossed the lake ( $P = 0.0016$ ).*

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## INTRODUCTION

Theoretical analyses of the energetic costs of flight have identified optimal strategies for birds that migrate long distances (reviewed by Richardson, 1991; Alerstam and Hedenström, 1998). Migrating animals fly long distances on a limited amount of fuel. Hence, they may be under selection to fly at the maximum range velocity, which maximizes distance for a minimum required energy. The maximum range velocity is derived graphically by drawing a tangent from the origin to the U-shaped power curve for flight (Pennycuik, 1978). Because the origin of this tangent shifts negatively with the velocity of the tailwind (and positively with a headwind), the maximum range velocity is greater in a headwind and less in a tailwind relative to its magnitude in a still wind. If the migrant is capable of tailwind drift compensation and it is behaving optimally to minimize the energetic cost of flight, it is predicted to decrease its airspeed in the presence of tailwinds (and increase it in headwinds). For migrating birds, adjustment of airspeed for tailwinds has been demonstrated repeatedly (see citations by Alerstam and Hedenström, 1998).

The prediction of tailwind drift compensation based on the U-shaped power curve for bird flight should also be applicable to at least a few migrating insects. A power curve for flight, in which the power required to fly increases with velocity above the minimum power velocity, has also been demonstrated in Lepidoptera and Odonata (Dudley and DeVries, 1990; Wakeling and Ellington, 1997). Tailwind drift compensation would support predictions derived from optimality models.

However, tailwind drift compensation has rarely been studied in migrating insects (Srygley and Oliveira, 2001). Migrant sulfur butterflies *Aphrissa statira* did not compensate for tailwind drift when flying over a lake (Srygley *et al.*, 1996). Female cloudless sulfur butterflies *Phoebis sennae* adopted this strategy of minimizing energy consumption when flying over the Caribbean Sea. However, male cloudless sulfurs did not reduce their flight speed to minimize energy consumption. Instead, they held flight speed constant so that they would minimize the time to reach the destination (Srygley, 2001a).

Tailwind drift compensation also has important ramifications for measuring flight speeds of insects in nature (e.g., Srygley and Dudley, 1993; Dudley and Srygley, 1994). If insects adjust their airspeeds for ambient tailwinds, then airspeed will be dependent on the environmental context in which it is measured and comparisons of airspeeds among taxa will require adjustment for tailwinds first.

A second form of drift compensation is the adjustment of heading to offset crosswind drift. Alerstam (1979) modeled the optimal crosswind drift compensation based on the ability of the animal to navigate as opposed to

migrate with a fixed compass orientation. Assuming that the migrants are capable of navigating to a particular destination, full compensation minimizes flight duration and energy consumption when winds are constant during the migration. When winds vary, an increase in the degree of compensation from none to part to full as the migrant approaches its destination minimizes flight duration and energy consumption. The same predictions arise from models that assume the migrants orient toward a preferred compass direction. However, in this case, risk of drift away from suitable destination areas increases because of an inability to navigate.

Recently, Srygley *et al.* (1996) examined crosswind drift compensation in Lepidoptera flying over a lake where landmarks were visible on the horizon. Individual butterflies migrating across Lake Gatún, Panama, adjusted their heading to hold the ground track despite changes in crosswind drift that each experienced as it crossed the lake. In comparison, there was no evidence that *Urania* moths were able to compensate for wind drift. The study was unable to distinguish between full and part compensation for wind drift in butterflies. Identifying full or part compensation is important because full compensation is evidence for use of landmarks to compensate for crosswind drift, whereas part compensation is evidence for use of the vector motion of ripples on the water surface relative to the body axis (for further details, see Srygley *et al.*, 1996).

Compensating for tailwind and crosswind drift is particularly difficult over water, where not only the insect but the surface beneath the insect moves downwind (for discussion, see Srygley *et al.*, 1996; Srygley, 2001b). However, migrations over water provide a methodological advantage because, with sailboat navigation equipment mounted on a boat, insect orientation and velocity and ambient wind direction and velocity are measured simultaneously.

In this paper, I examine tailwind and crosswind drift compensation in two dragonfly species migrating across the isthmus of Panama. The ability to adjust flight velocity to maximize the range that an insect is able to fly is likely to be under strong natural selection in migrating dragonflies. I investigated five related questions. (1) Were the populations of two migrating dragonfly species, *Pantala hymenaea* (Say) and *P. flavescens* (Fabr.), oriented to a preferred track direction? (2) Among individuals, was the dragonfly's heading related to the crosswind prevalent at the time that it crossed the lake? (3) Within an individual, was each dragonfly capable of adjusting its heading to hold its ground track despite changes in crosswind drift that it experienced as it crossed the lake? (4) Among individuals, was the dragonfly's airspeed related to changes in tailwind? and (5) Finally, within an individual, did a dragonfly adjust its airspeed to compensate for changes in tailwinds as it crossed the lake?

## MATERIALS AND METHODS

### Study Organisms

The spot-winged glider *Pantala hymenaea* and the wandering glider *P. flavescens* (Odonata: Anisoptera: Libellulidae) are pantropically distributed and may migrate into the temperate zone as well (Russell *et al.*, 1998). *P. flavescens* migrates long distances immediately after emergence, often in association with monsoon fronts (Dumont and Verschuren, 1991). *P. hymenaea* has a pattern of migration similar to that of *P. flavescens*, however, their smaller body size may limit the distance that they travel relative to *P. flavescens*.

Between 10 September and 6 October 1997, R. Aizprúa and I sampled migrating insects in the region of the Panama Canal, principally on Lake Gatún. We observed *Pantala hymenaea* dragonflies flying easterly in the afternoon of 11 September and on 18 September. Both mass movements were coincident with the onset of a storm front to the west.

We classified the movement to be a migration because the dragonflies were observed flying in the same direction at two points that were spaced over a large distance. On 19 September, the dragonfly migration continued over Lake Gatún. On 20 September, dragonflies were flying toward approximately the same direction (70–80°) at Kobbe Beach and Venado Beach, which are near the mouth of the Panama Canal on the Pacific Coast and approximately 50 km from our site on Lake Gatún. *P. hymenaea* were remarkably difficult to capture flying over the lake, but we were able to capture two specimens on 25 September for identification. The data concerning *P. hymenaea* for this paper were collected on 25–26 September during migrations departing Barbour Point, where the lake is approximately 1.5 km wide.

On 3 October and 6 October, a dragonfly species that was similar in color, but larger and with more brown on the wings, was observed migrating noticeably higher above Lake Gatún (approximately 3 m, relative to 1–2 m for *Pantala hymenaea*). We did not succeed in capturing one of these dragonflies from the boat, but I am reasonably certain that the second species was *P. flavescens* based on differences in color and size relative to *P. hymenaea*, its renown as a migrant in this region, and comparison with specimens in the dry collection at the Smithsonian Tropical Research Institute. The data concerning *P. flavescens* for this paper were collected near Barbour Point on these two dates in October.

I lack the data necessary to generate aerodynamic power curves specifically for *Pantala hymenaea* and *P. flavescens*. Therefore, I have based their shapes on that derived for the dragonfly *Sympetrum sanguineum* in Britain (Wakeling and Ellington, 1997). For *S. sanguineum* (body mass, 111–139 mg;

wing length, 26.4–29.4 mm), the minimum power velocity was approximately 1–1.3 m/s. Aerodynamic power increased at velocities higher than the minimum power velocity to form either a J-shape or the right-hand half of a U-shape power curve (see also Ellington, 1991). *P. hymenaea* is approximately twice as large as *S. sanguineum* ( $n = 2$  males: mass, 235–279 mg; wing length, 41.6 mm). A difference in body size affects the position of the curve relative to the axis origins, but it should not affect the general shape of the power curve, upon which the theoretical prediction of tailwind drift compensation is dependent.

### **Individual Dragonfly Airspeed, Track Direction, Heading, and Local Wind**

Dragonflies were intercepted while flying over Lake Gatún and followed in a 13-ft Boston Whaler powered by a 30-hp outboard motor until an even pace was maintained parallel to the flight direction. We sampled dragonflies flying over the water on 18–19 and 22–29 September and 2–3 and 6 October 1997. Sampled insects remained within 1–3 m of the water surface and progressed forward steadily.

Boat heading was measured with a flux-gate compass (Raytheon heading sensor M 92649) mounted on the boat deck, approximately 0.5 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 that extended from the top of an L-shaped mast. The mast was attached to the bow to position the anemometer between 1.5 and 2 m above the water surface and well in front of the boat to avoid wind shear generated by the bow. Boat speed, boat heading (magnetic), 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 (Model 4321). Positional coordinates ( $\pm 45$  m), speed over ground, and true course over ground were also collected (in NMEA) from a Garmin global positioning satellite (GPS) receiver. All 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 10 s using a customized DOS BASIC program (A. Trimble, unpublished application). The calibration of the navigation equipment is provided in the Appendix. Because *P. flavescens* flew approximately 1 m higher than the anemometer, I assumed a logarithmic increase in speed with height

(Gill, 1982). The resulting increase in wind speed for *P. flavescens* averaged  $5.3 \pm 0.2\%$  (SD) of that measured while tracking this species.

### Vector and Statistical Analyses

Groundspeed and track for the dragonflies and ambient wind speed and direction were sampled on 25 and 26 September, when *Pantala hymenaea* was migrating, and on 3 and 6 October, when *P. flavescens* was migrating. I calculated each dragonfly's heading and airspeed with a standard wind drift vector analysis (cf. Liechti *et al.*, 1994).

Airspeed may be investigated relative to the head- or tailwind component of groundspeed (e.g., Block and Bruderer, 1982; Williams *et al.*, 1986; Srygley, 2001a) or the change in speed due to wind (groundspeed minus airspeed [Pennycuick, 1978; Alerstam, 1985; Alerstam *et al.*, 1993]). A more refined model (Liechti *et al.*, 1994) for simultaneous adjustment for tailwind and crosswind drift may be applied when the flying animal compensates for crosswind drift. In this model, an organism behaving optimally to maximize 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 to compensate for tailwinds (as measured by the difference between groundspeed and airspeed). To be consistent with Liechti *et al.* (1994), I calculated the tailwind as the difference between groundspeed and airspeed, and I evaluated airspeed with a stepwise regression analysis on tailwind speed and the inverse of the cosine of the drift angle. For completion, I also report the results for airspeed regressed on the tailwind component of groundspeed.

In all other analyses, I applied an analysis of covariance (ANCOVA) using JMP (version 3.0; SAS Institute Inc.) to test for differences among the sampling dates in track orientation covaried for time during the day. Because only one dragonfly was measured on 6 October, *P. flavescens* on 3 and 6 October were combined. Track direction changed over time on 25 September but not on the other dates (see Results), and so for the analyses of wind compensation, I tested for differences in slopes and intercepts among the dates with ANCOVA.

To evaluate compensation for crosswinds or tailwinds at the population level, I regressed mean heading or mean airspeed on the mean ambient drift or tailwind, with each individual serving as a single observation. To evaluate compensation for crosswind drift or tailwind drift within each individual, I used the changes in ambient winds that resulted from insects moving between windward and leeward sides of land masses. The duration of the flight sequences ranged from 90 to 350 s. I subtracted the mean heading or airspeed during the first half of each flight sequence from that during the second half

of the flight sequence. I then compared this change in heading ( $\Delta$ heading) or  $\Delta$ airspeed with the change in mean drift ( $\Delta$ drift) or  $\Delta$ tailwind, respectively, between the two halves of the run.

I regressed the dependent variable (heading, airspeed, change in heading, or change in airspeed) on the covariate (crosswind drift, tailwind velocity, change in crosswind drift, or change in tailwind velocity) with ANCOVA and determined a significant difference in slopes by a significant interaction between the independent factor (sampling date) and the quantitative factor (crosswind drift or tailwind drift). If insignificant, I pooled variances due to the interaction and error and tested for differences in the dependent variable (heading or airspeed) among the dates following adjustment for the covariate. In this second model, if sampling date was not a significant factor, I pooled the data for all of the dates (including the two species) and present the regression model and probabilities for the relation of the dependent variable to its respective covariate.

## RESULTS

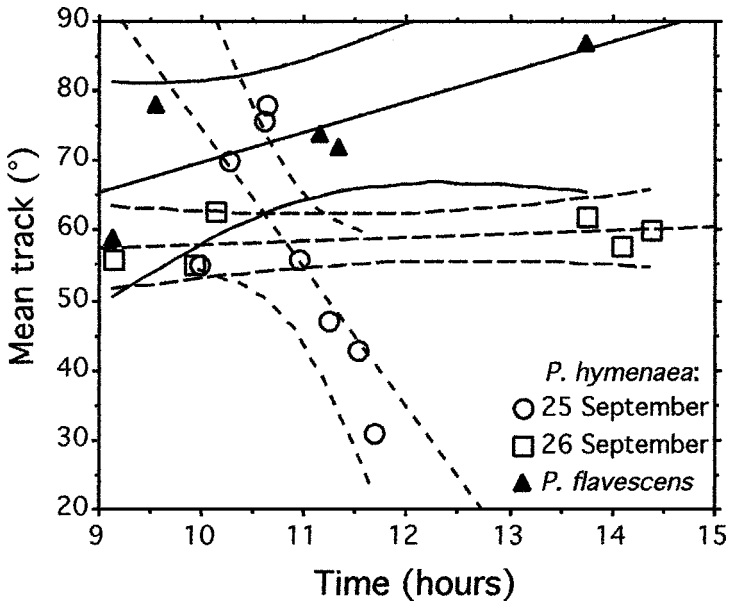
### Orientation Over the Course of the Day

The slopes of the regressions of the track directions on time were significantly dependent on the data (Fig. 1;  $P = 0.009$ ). Analyzing each date separately, the track direction of *Pantala hymenaea* on 25 September decreased significantly with time of day ( $P = 0.047$ ), whereas that on 26 September did not change significantly ( $P = 0.45$ ). The mean track directions for *P. hymenaea* on the two dates were not significantly different (25 September [95% confidence limits; CL], 52–62°; 26 September, 55–63°). *P. flavescens* maintained a constant track direction over the course of the day as well ( $P = 0.125$ ). *P. flavescens*' track was significantly more easterly than that for all *P. hymenaea* combined (mean  $\pm$  SE, 74  $\pm$  5°;  $P = 0.0082$ ).

The difference between dates is evidence that *Pantala hymenaea* dragonflies were directionally oriented on some days but not directionally oriented on others. Hence, in the following analyses, wind compensation was analyzed with date as an independent variable. If date was not a significant factor, then I pooled dates. Bear in mind that *P. hymenaea* on 25 September and 26 September composed two date classes, and *P. flavescens* on 3 and 6 October composed the third date class.

### Crosswind Drift Compensation

The slopes of the regressions of headings on crosswind drift were significantly dependent on date ( $P = 0.0005$ ). For *P. flavescens*, heading was



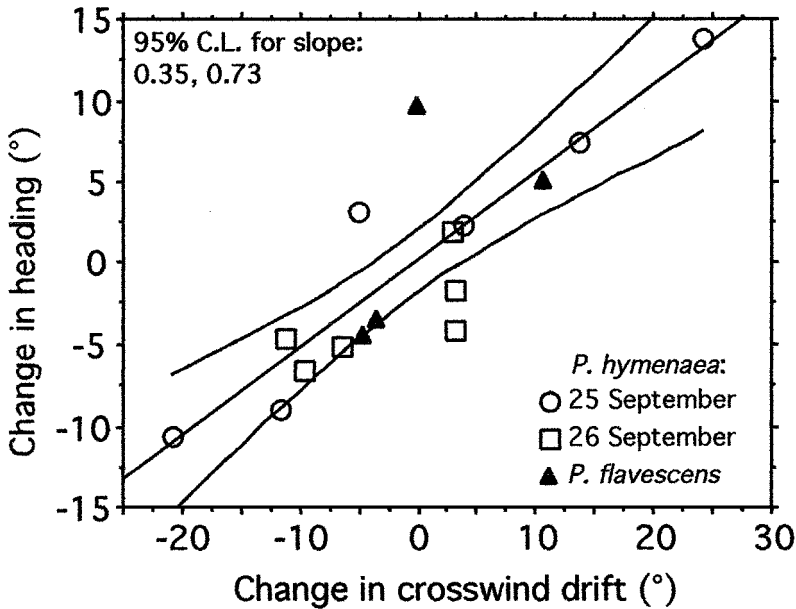
**Fig. 1.** The regressions of mean track directions of *Pantala hymenaea* on two dates and *P. flavescens* flying over Lake Gatún over the course of the day. Each point is an individual dragonfly. Corresponding dashed or solid curves show the 95% confidence limits. The slope of track direction on time was not significantly different from zero for *P. hymenaea* on 26 September or *P. flavescens*. On 25 September, the track of *P. hymenaea* drifted downwind.

significantly dependent on drift (heading =  $75^\circ + 0.75$  drift;  $n = 5$ ;  $P = 0.014$ ). The slope of heading on drift was not significantly different from full compensation (predicted slope,  $b = 1$ ; observed 95% CL, 0.29–1.21).

For *P. hymenaea* on 25 September, heading was not significantly dependent on drift (heading =  $111^\circ - 0.35$  drift;  $n = 8$ ;  $R^2 = 0.41$ ,  $P = 0.086$ ). The slope of heading on drift was not significantly different from that for no compensation (predicted slope,  $b = 0$ ; observed 95% CL,  $-0.77$ – $0.07$ ). However, for the same species on 26 September, heading was significantly dependent on crosswind drift (heading =  $59^\circ + 1.0$  drift;  $n = 6$ ;  $R^2 = 0.85$ ,  $P = 0.009$ ). The slope of heading on drift was not significantly different from that for full compensation (95% CL, 0.41–1.60). Although the mean track directions were not significantly different for the two dates, the range of track directions differed as a result of this difference in crosswind drift compensation (see Fig. 2).

Dragonflies individually adjusted for changes in crosswind drift. The slopes for change in heading ( $\Delta$ heading) on changes in crosswind drift





**Fig. 2.** The regression and 95% confidence intervals for change in heading of individual dragonflies relative to the change in crosswind drift while each flew across Lake Gatún. The data for *Pantala hymenaea* and *P. flavescens* were pooled, because the regression lines were not significantly different. The intercept was not significantly different from zero. Each point represents compensation in an individual dragonfly. C.L. confidence limits.

( $\Delta$ crosswind drift) did not differ among dates ( $P = 0.708$ ), nor did mean  $\Delta$ heading differ among the dates following adjustment for  $\Delta$ crosswind drift ( $P = 0.338$ ). Pooling the data for *Pantala* spp.,  $\Delta$ heading increased significantly with  $\Delta$ crosswind drift (Fig. 2;  $\Delta$ heading =  $0.19^\circ + 0.54 \Delta$ crosswind drift;  $n = 16$ ;  $R^2 = 0.73$ ,  $P = 0.0001$ ). The slope of  $\Delta$ heading on  $\Delta$ crosswind drift did not overlap with that for full compensation. Hence, there is strong evidence for part compensation for crosswind drift within individuals.

### Tailwind Drift Compensation

Using the incremental increase in speed with tailwinds as the measure of tailwind velocity (e.g. groundspeed minus airspeed), the slopes of the regressions of airspeed on tailwind velocity did not differ significantly among the dates ( $P = 0.605$ ), nor did the mean airspeeds differ following adjustment for tailwinds ( $P = 0.388$ ). Pooling the dragonflies, airspeed declined significantly and linearly with the velocity of the tailwind (Fig. 3). Among

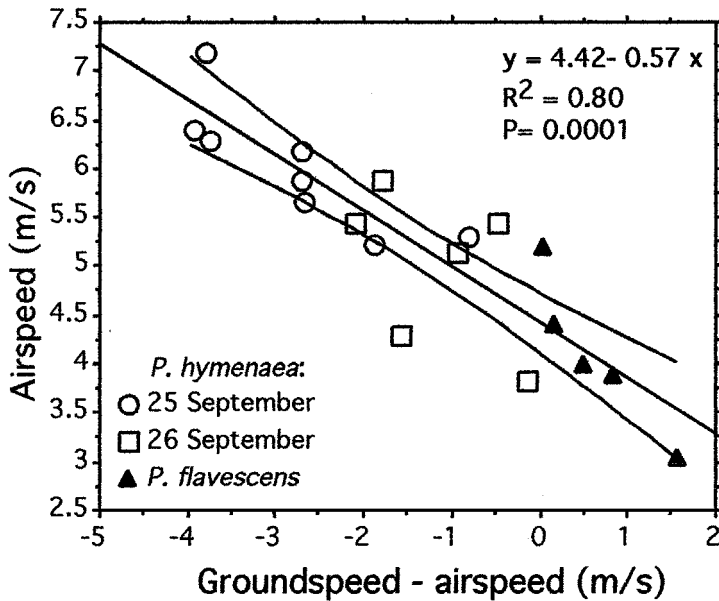
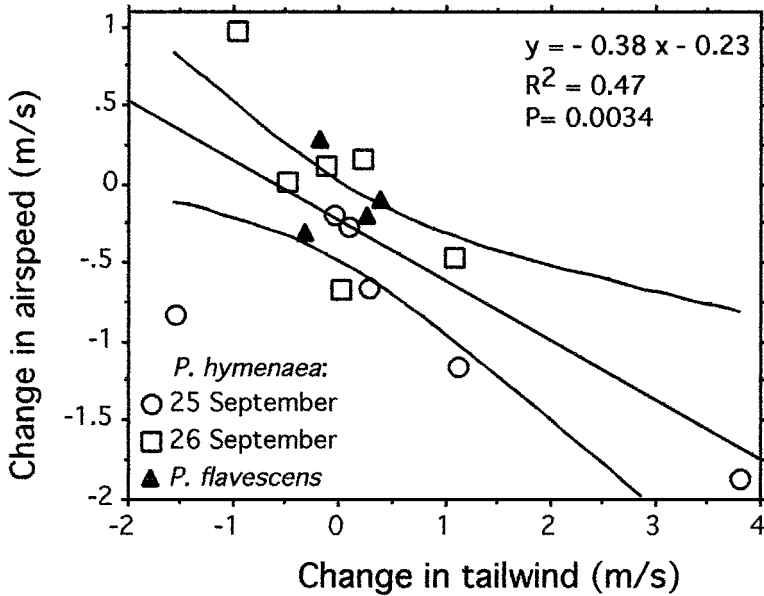


Fig. 3. The regression and 95% confidence intervals for airspeed on tailwind drift velocity. The data for *Pantala hymenaea* and *P. flavescens* were pooled, because the regression lines were not significantly different. Each point represents an individual dragonfly.

individuals, dragonflies adjusted their airspeed for tailwind velocity in less than a one-to-one fashion (95% CL,  $-0.97$  to  $-0.48$ ).

Tailwind and crosswind drift ( $1/\cos$  drift) were not significantly associated ( $P = 0.128$ ). Hence an analysis of the dragonflies' adjustment of airspeed for both tailwind and crosswind drift is justified. Airspeed was not associated with crosswind drift ( $P = 0.119$ ) following adjustment for tailwind drift ( $P < 0.0001$ ). Therefore, I was unable to demonstrate that dragonflies simultaneously adjust their airspeed for both tailwinds and crosswind drift with this qualitative analysis. Without a power curve for *Pantala*, a more rigorous test of the model is not possible.

Using the tailwind component of groundspeed as the measure for tailwinds, the results were qualitatively identical. The slopes of the regressions of airspeed on tailwind velocity did not differ significantly among the dates ( $P = 0.736$ ), nor did the mean airspeeds differ following adjustment for tailwinds ( $P = 0.917$ ). Pooling the dragonflies, airspeed declined significantly and linearly with the velocity of the tailwind ( $y = 5.04 - 0.77x$ ). Among individuals, dragonflies adjusted their airspeed for tailwind velocity in less than a one-to-one fashion (95% CL,  $-0.97$  to  $-0.48$ ).



**Fig. 4.** The regression of the change in airspeed on the change in tailwind velocity experienced by each dragonfly while crossing the lake. The data for *Pantala hymenaea* and *P. flavescens* were pooled, because the regression lines were not significantly different. The intercept was not significantly different from zero. Each point represents compensation in an individual dragonfly.

Within individuals over the lake, the slopes relating changes in airspeed ( $\Delta$ airspeeds) to changes in tailwinds ( $\Delta$ tailwinds) did not differ significantly among the dates ( $P = 0.532$ ), and mean  $\Delta$ airspeeds did not differ among dates following adjustment for  $\Delta$ tailwinds ( $P = 0.052$ ). Pooling the data for *Pantala* spp.,  $\Delta$ airspeed declined significantly with  $\Delta$ tailwind (Fig. 4). The intercept was not significantly different from zero. Therefore, individual dragonflies adjusted their airspeed for changes in tailwind velocity in less than a one-to-one fashion (95% CL,  $-0.61$  to  $-0.15$ ).

The change in tailwind and the change in crosswind drift that an individual dragonfly experienced were not significantly associated ( $n = 16$ ;  $P = 0.162$ ). Hence I conducted an analysis of the dragonflies' adjustment of airspeed for both tailwind and crosswind drift. The change in airspeed was not significantly associated with crosswind drift following adjustment for tailwind drift ( $n = 16$ ;  $r = 0.72$ ,  $P = 0.002$ ). Therefore, I was unable to demonstrate that individual dragonflies simultaneously adjust their airspeed for both tailwinds and crosswind drift.

Using the change in the head- or tailwind component as the independent variable, the regression line and confidence intervals for the slope ( $y = -0.38x - 0.23$ ; 95% CL,  $-0.61$  to  $-0.15$ ) were not significantly different from that derived by using groundspeed less airspeed as the independent variable. Hence, there is evidence for compensation for tailwind velocity within individuals.

## DISCUSSION

*Pantala* dragonflies compensated for both crosswind and tailwind drift when flying over Lake Gatun. As each dragonfly flew across the lake, it flew through leeward and windward regions. Dragonflies behaviorally adjusted their headings to compensate in part for the change in crosswind drift. They also behaviorally adjusted their airspeeds to compensate for the change in tailwind velocity. For migrating insects, this is the first evidence for tailwind compensation as predicted by optimality models (Pennycuick, 1978; Alerstam and Hedenström, 1998). Airspeed ranged from approximately 3.1 to 5.2 m/s in *P. flavescens* and 3.9 to 7.2 m/s in *P. hymenaea*, depending on the tailwind velocity. Adjusting for tailwind velocity, there was no difference in airspeed among the species. Airspeed with no tailwind was 5.0 m/s for both species. This result emphasizes the importance of making comparisons among species with tailwind-adjusted airspeeds.

Within individuals, *Pantala* demonstrated significant part compensation for crosswind drift. The degree of compensation, estimated to be 35–73%, may be used to distinguish among mechanisms of wind drift compensation (see discussion by Srygley *et al.*, 1996). Part compensation is evidence for use of ripples and waves on the lake surface as a ground reference.

Over land, the use of a ground reference, i.e., the motion of the ground relative to the insect's longitudinal body axis, may be used to adjust for crosswind drift. The angle relative to the desired track direction with which the ground passes beneath the insect is the course correction required to hold the track direction true. When over water, use of a ground reference will result only in part compensation, because waves on the water surface also blow downwind, drifting more slowly than the insect (Alerstam and Pettersson, 1976). Part compensation is less energetically costly than full compensation, but unless they are able to navigate, the dragonflies would be less likely to reach a goal than they would be if they compensated fully.

A decrease in airspeed with tailwind velocity as predicted from Pennycuick's (1978) model of maximum range velocity, was demonstrated both within and among individual dragonflies. The slopes of the lines differed significantly from a slope that would hold groundspeed constant (slope,

$b = -1$ ), as observed in honeybees (Heran, 1956; cited by Esch and Burns, 1996). However, if they were using the ground as a reference, the dragonflies would have undercompensated for tailwind drift because the ground, i.e., the surface of the water, was moving with the wind (a similar result occurs in honeybees flying over water [Esch and Burns, 1996]). Alternatively, the dragonflies may be adjusting airspeed to fly at the maximum range velocity.

Lack of support for Liechti's model for sidewind compensation (Liechti *et al.*, 1994) should not be considered conclusive for two reasons. First, the model assumes that dragonflies were compensating fully for crosswind drift. Here, I demonstrate part compensation, and hence the model becomes more difficult to evaluate. Second, Liechti's model is best evaluated with a quantitative prediction of changes in aerodynamic power with airspeed. Further evaluation of this model will have to await an aerodynamic power curve for the *Pantala* spp.

*Pantala hymenaea* migrated frequently into headwinds, whereas *P. flavescens* migrated exclusively with tailwinds (see Fig. 3). Selection of tailwinds greatly reduces the energetic requirements for flight and increases the distances that could be reached by migrating *P. flavescens*. Additional data are required to elucidate whether this difference between the species amounts to a difference in selection of winds.

The associations of dragonfly migrations with storm fronts has been noted in the eastern United States (Russell *et al.*, 1998), as well as in this paper. In the temperate zone, the migrants follow behind the cold front, whereas in Panama, the migrants were just ahead of the front. *Pantala* dragonflies may use the leading edge of storms to forecast newly formed ephemeral pools in which they reproduce (Dumont and Verschuren, 1991).

Over the course of the day, individual *P. flavescens* adjusted their headings and compensated for crosswind drift to maintain a constant track direction. *P. hymenaea* maintained a constant heading and drifted downwind on one day and compensated for crosswind drift maintaining a constant track direction on the next. As a result, the track directions of *P. hymenaea* changed consistently with crosswind drift from  $78$  to  $31^\circ$  on the first day, although the mean track direction was no different from the second day. On 25 September, wind direction rotated from  $150$  to  $110^\circ$  at a rate of  $19^\circ/\text{h}$  as wind speed increased  $1.3 \text{ m/s/h}$ . Crosswind drift also increased  $15^\circ/\text{h}$ . On the following day, wind direction remained more constant,  $148 \pm 5^\circ$ , and wind speeds were significantly lighter ( $P = 0.049$ ) and increased only  $0.3 \text{ m/s/h}$ . Given that the mean track directions were not different between the two dates, the dragonflies appear to have overcompensated for drift in the lighter winds of early morning and then drifted as the wind speed increased.

To date, we know very little about dragonfly migrations (see Russell *et al.*, 1998), yet migratory dragonflies are likely to affect predator-prey interactions on both local and continental geographic scales. Migrating dragonflies are a prey item for birds (e.g., broad-winged hawks [Bildstein, 1999], Swainson's hawk [Rudolph and Fisher, 1993]). Because dragonflies are predaceous in both the aquatic larval and the aerial adult stages, they also serve as important control agents. Wind drift compensation provides insight into where and how dragonflies migrate. Our understanding of the abilities of dragonflies to compensate for wind drift will improve our ability to map flyways and identify corridors of natural habitat for protection (see also Srygley *et al.*, 1996).

## APPENDIX

The navigation equipment was calibrated on 18 September when the wind speed was 0–0.5 m/s. When the boat was running forward, the apparent wind direction was adjusted so that it was 0° relative to the boat heading. The anemometer was calibrated by varying the boat speed and comparing the apparent wind with readings from a Kurtz handheld unidirectional anemometer that had been calibrated within the past year. The flux-gate compass was calibrated by directing the bow of the boat toward a landmark and matching the heading with the direction measured by the handheld flux-gate compass. Boat speed was calibrated by directing the boat in a constant direction and comparing the boat speed with readings from the apparent wind speed read from the Kurtz anemometer.

When the boat was piloted in a straight line on 18 September and again on 29 September, a comparison of mean boat speed with mean speed over the ground from the GPS demonstrated that the two measures when averaged over 30 s were always within 0.75 m/s of one another but more typically differed by less than 0.25 m/s.

To estimate errors in wind speed and wind direction, two methods were employed. First, I measured wind speed and wind direction while pacing four insects between 1100 and 1130 h on 6 October 1997 (wind speed ranged from 0.5 to 2.75 m/s). I compared these speeds and directions to measurements when the boat was standing at the end of each run (standing wind speeds were 0.5–1.0 m/s higher than mean running wind speeds). Standing wind speeds were within 0.5 m/s of wind speeds measured simultaneously with a Kurtz handheld unidirectional anemometer. Hence, error in wind speed was less than 1.0 m/s. Corresponding measures of average wind direction differed by 10 to 40°. Large differences may have been due to rapidly shifting winds that are typically observed under partial cloud cover during midday hours

or movement between the leeward and windward sides of land masses while pacing insects.

Second, average wind speeds and directions while the boat was running were compared to those taken while standing immediately after capturing the insect on 25 September, 26 September, and 3 October. Running wind speeds were always within the variation in standing wind speeds, and running wind directions were within 20° of standing wind directions. From these data, I conclude that error in wind speed was less than 1.0 m/s and error in wind direction was less than 20°.

In a steady wind, wind speed increases to the logarithm of height above the water (Gill, 1982). Dragonflies were migrating between 1 and 3 m, and the anemometer was positioned at a height of 1.5–2 m. From data collected on boundary layer winds at 0.5–16 m in Australia (Clarke *et al.*, 1971), I empirically derived a formula for predicting wind velocities at different heights from that measured at 2 m:  $v_h = v_2 + 0.13v_2(\ln h - \ln 2)$ , where  $v_h$  is the wind velocity at height  $h$  and  $v_2$  is the wind velocity at 2 m (the height of the anemometer). This formula predicted 100% of the variance in 40 wind velocities sampled from 0.5 to 16 m (at five of the times listed in Table I and all of the times listed in Table II at station 5 of Clarke *et al.* [1971]). Wind speeds at 1 m are predicted to be 9% lower than that measured at 2 m, whereas those at 3 m are 5.3% higher.

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