

DO NEOTROPICAL MIGRANT BUTTERFLIES NAVIGATE USING A SOLAR COMPASS?

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Summary

Many tropical butterfly species are well-known for their migratory behaviour. Although these insects can maintain a constant direction throughout the day, the physiological mechanisms of orientation are unknown. It has been argued that tropical migrant butterflies must use a time-compensated sun compass to accomplish their journey, but the crucial experimental manipulations to test this hypothesis have not been conducted. This study reports the results of clock-shift experiments performed with two species of migrating butterflies (Pieridae: *Aphrissa statira* and *Phoebis argante*) captured during flight across Lake Gatún, Panamá. The observed constant flight bearing of natural controls suggests that these species are capable of performing time-compensated celestial navigation. Our clock-shift experiments suggest that a sun compass is involved. Individuals submitted to a 4 h advance shift took

significantly different mean orientations on release compared with control butterflies. The direction of this difference was consistent with the use of a sun compass. The magnitude was approximately half the predicted value if the vanishing bearing of released butterflies was used as the variable to evaluate the effect of time-shifting and approximately three-quarters of that predicted if the estimated heading was the variable used. Mean vanishing bearings of control and experimental butterflies did not correspond to predicted values. This difference can be attributed largely to the combined effects of wind and handling.

Key words: butterfly, migration, clock-shift, navigation, orientation, sun compass, *Aphrissa statira*, *Phoebis argante*.

Introduction

Navigation is usually required to ensure that long-distance migrants reach a particular destination. Two forms of navigation, orientation to a fixed compass bearing and goal-orientation (i.e. true navigation and goal-finding using innate vector programs or navigational maps; Berthold, 1993), require the use of an orientation cue at a great distance (essentially infinite) relative to the position of the animal. For diurnal migrants, such as the butterfly species in the present study, the sun or the geomagnetic pole may provide such a cue. Dependence on one or both of these cues becomes mandatory if migrants must traverse areas where locally visible landmarks are limited and where the topography and wind conditions are variable (Dingle, 1996). In Panamá, *Aphrissa statira* butterflies flying over a lake compensated, at least in part, for being blown off course by the wind. These results are consistent with either form of navigation outlined above (Srygley *et al.* 1996). On a larger scale, the particularly complex land-mass of Central America may additionally demand precise control of direction to avoid migrants being lost at sea.

The use of the sun as an orientation cue has been demonstrated in many vertebrate and invertebrate species

(Santschi, 1911; von Frisch, 1967; Able, 1980; Wehner, 1984; Waterman, 1989; Wehner *et al.* 1996). In its simplest form, sun orientation does not incorporate compensation for time of day, so that the animal's direction of movement changes with the apparent movement of the sun (Baker, 1968*a,b*, 1969; Wallraff, 1981). The more complex time-compensated sun compass enables a constant direction to be maintained throughout the day. Time-compensation is achieved using an internal circadian clock set to the local time by entrainment to the natural light:dark cycle. Such a mechanism is best demonstrated by clock-shift experiments, in which induced phase shifts in the circadian endogenous clock cause predictable changes in orientation (Emlen, 1975; Able, 1980; Wallraff, 1981; Wehner, 1984; Schmidt-Koenig *et al.* 1991*a*).

Although many butterfly species are well-known migrants and are often observed to maintain a constant bearing throughout the day (Williams, 1930; Nielsen, 1961; Johnson, 1969; Schmidt-Koenig, 1985; Walker and Riordan, 1981; Walker, 1985; Oliveira, 1990), until recently the source of their compass information remained unknown (Able, 1980; Baker, 1984; Wehner, 1984; Schmidt-Koenig, 1985; Walker

and Littell, 1994; Brower, 1996; Dingle, 1996). Able (1980) and Baker (1984) argued that long-distance migrant butterflies (e.g. the monarch *Danaus plexippus*; see Brower, 1995) must use a time-compensated sun compass to accomplish their journey. Observations that particularly suggested the use of a sun compass were made by Baker (1968*a,b*, 1969) for short-distance migrant butterflies in Europe, by Kanz (1977) for *D. plexippus* in experimental cages, and by Oliveira (1990) for migration of pierids (including the species reported in the present study) in the eastern Brazilian Amazon. These studies present examples in which butterflies showed only partial time-compensation (or none at all) and their orientation tended to follow the sun's azimuth (the compass bearing of the nearest point on the horizon to the sun). Recent work by Perez *et al.* (1997) has provided experimental clock-shift evidence for a sun compass in monarch butterflies.

In central Panamá, butterflies of the species *Aphrissa statira* (Cramer), *A. boisduvalii* (Felder), *Phoebis argante* (Fabricius), *P. trite* (L.), *P. sennae* (L.), *P. philea* (L.), *Marpesia chiron* (Fabricius) and *M. petreus* (Cramer) are routinely observed in migratory flight from mid May to late July (for *Aphrissa* spp., see Fig. 1). Migrating butterflies appear just after the onset of the rainy season, and south-southwest is the predominant migratory direction (Fig. 2). A map of the flyway across the isthmus of Panamá for *Aphrissa* spp. is shown in Srygley *et al.* (1996). The daily peak of migratory activity occurs between 10:00 and 12:00h, although activity may last from 09:00 to

15:00h or later on sunny, hot days (Fig. 3). The present study focused on two species in this migratory system, *A. statira* and *P. argante* (Pieridae: Coliadinae). We first determined whether naturally migrating butterflies maintain a constant direction throughout the day. Using experimental manipulation of the butterflies' endogenous clock, we then investigated whether they use the sun as an orientation cue and whether they adjust their flight orientation to compensate for the sun's apparent movement.

Materials and methods

Field and laboratory work were conducted at Barro Colorado Island, Panamá (9°10' N, 79°51' W), in May–July of 1991–1996. To determine whether time of day had an effect on the flight direction of naturally migrating butterflies, we intercepted the flight path and measured the track direction of 1739 *Aphrissa* spp. and 296 *P. argante* flying across Lake Gatún with the aid of a Suunto KB-14 sighting compass. A 30 horsepower motorboat was used to follow each individual. We regressed flight direction on time of day (h). To meet the assumption of linear regression analysis, values more than $\pm 90^\circ$ from the mean (210° for *Aphrissa* spp. and 196° for *P. argante*) were excluded (7% of the total for *Aphrissa* spp. and 5% for *P. argante*). To control for the effect of cross-winds, we excluded flight directions measured when wind speed exceeded 2 m s^{-1} (52% of the total for *Aphrissa* spp. and 49% for *P. argante* for those individuals within $\pm 90^\circ$ from the

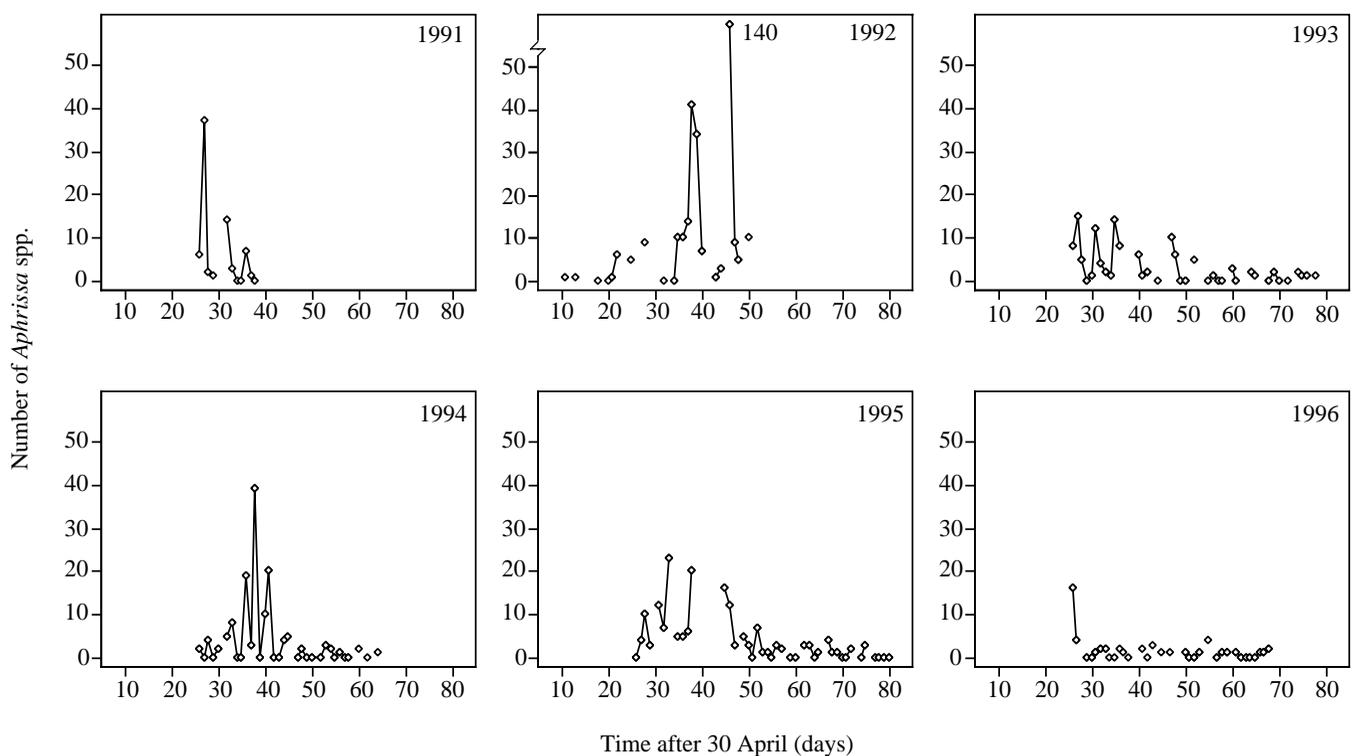


Fig. 1. Observed maximum number per minute of migrating *Aphrissa* spp. butterflies flying south-westerly across a 300m transect on Lake Gatún, Panamá, during May–July of 1991–1996. A solid line connecting the points indicates successive daily counts. We pooled data for *A. statira* and *A. boisduvalii* because it is difficult to distinguish these two species during free flight.

respective means). This approach is justified by the observation that these species may compensate fully for cross-wind drift when wind speed does not exceed 2 m s^{-1} [for *Aphrissa* spp.,

$y=215-0.92x$, where y is heading (in degrees) and x is drift (in m); 95 % confidence intervals $-1.61, -0.23$; $N=63$; $P<0.009$; see methods in Srygley *et al.* 1996]. Wind direction and speed

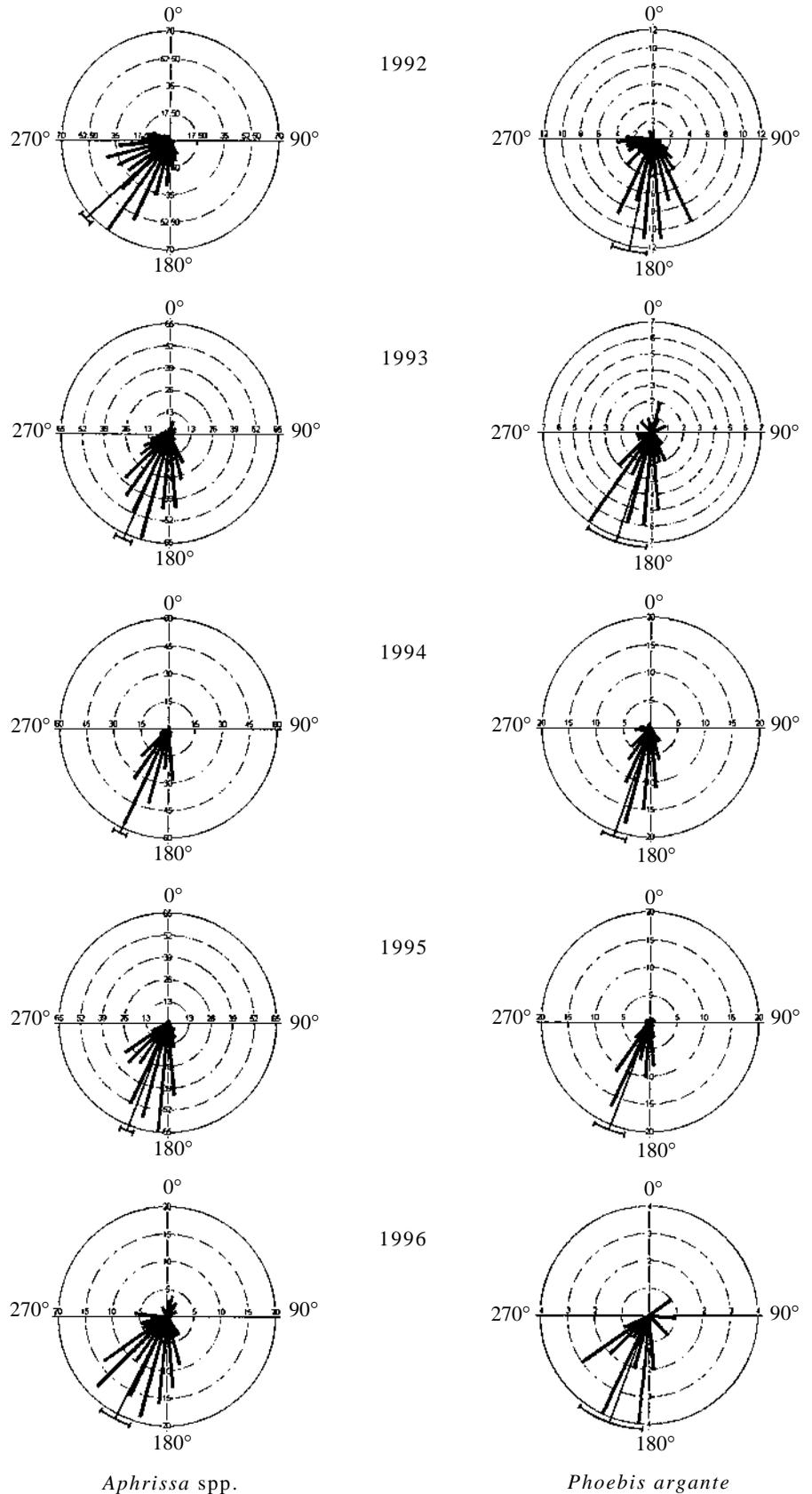


Fig. 2. Migratory direction of free-flying *Aphrissa* spp. and *Phoebis argante* butterflies across Lake Gatún in 1992–1996. Length of radii corresponds to the number of observations within each 10° arc. An arc outside each circle shows the mean direction with 95 % confidence intervals. The scale is different in each diagram, because of differing sample sizes. The outer arc represents 70, 65, 60, 65 and 20 individuals for *Aphrissa* spp. for 1992–1996, respectively, and 12, 7, 20, 20 and 4 individuals for *P. argante*. Here, and in subsequent figures, bearings are given with reference to magnetic north. Local magnetic declination between 1992 and 1996 was negligible (range approximately $51'$ to $1^\circ 28'$; see Peddie, 1993) relative to measurement imprecision.

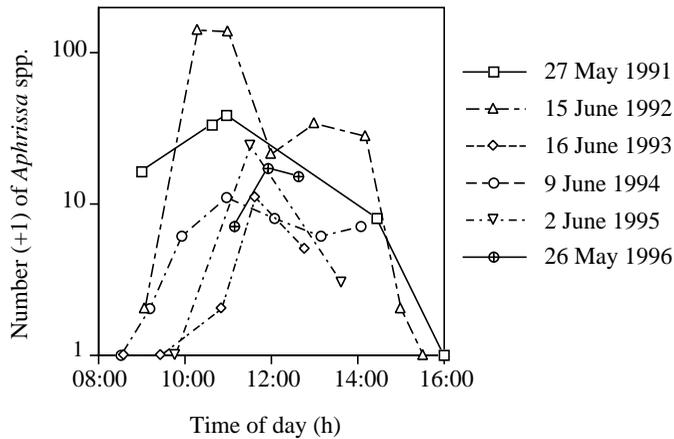


Fig. 3. Number of migrating *Aphrissa* spp. butterflies flying south-westerly across a 300 m transect on Lake Gatún at different times on the day of highest migration rate of each year between 1991 and 1996 (see Fig. 1). For 1994, data for the day of second highest migration rate are plotted because for the day of highest rate we did not have samples at different times of day. One (1) was added to individual counts to allow logarithmic representation of counts that yielded no individuals. Migratory activity normally occurred from 09:00 to 15:00 h with a peak between 10:00 and 12:00 h, but varied across days according to the prevailing weather. Activity often ceased in the early afternoon owing to a rapid deterioration in the weather that normally occurs at this time of day in this area (see Windsor, 1990).

were measured every 2–5 min using a weathervane and an anemometer (TSI, model 1650).

In the present study, track refers to the path the butterflies take when migrating naturally (before handling), and track direction refers to the direction of that path relative to magnetic north. Flight direction is used for both track direction before handling and vanishing bearing following release (see below).

All butterflies used in the clock-shift experiments were captured during flight across the lake. Before capture was attempted, the butterfly's track direction was measured. Each captured butterfly was placed in a numbered glassine envelope within which it was kept between the time of capture and the time of release. The butterflies captured on each day were sorted by species and into pairs of individuals matched as closely as possible for original flight direction, body mass, wing wear and sex. Individuals from each pair were then assigned randomly to control or experimental treatments.

Experimental individuals were maintained in an environmental chamber (Percival 1-35LL) set to a light:dark photoperiod 4 h ahead of the true solar time (4 h advance shift). Control individuals were kept in a second identical chamber in which the light:dark cycle was in synchrony with the natural cycle. Temperature in the chambers was set to 28 °C during the light phase and 25 °C during the dark phase. These values approximately match those measured in a forest clearing on Barro Colorado Island at the same time of year (Windsor, 1990). To compensate for natural twilight, we set the light phase to begin 10–15 min prior to sunrise (objective and

subjective time for controls and experimentals, respectively) and to end 10–15 min after sunset. Control and experimental butterflies were hand-fed 20% honey solution once daily in their objective and subjective afternoon, respectively. Approximately 15% of the individuals died during the treatment, 62% of which were in the experimental group. This latter percentage is not significantly different from 50% (binomial test with normal approximation, $Z=1.60$, $0.10 < P < 0.20$).

After 2–4 days under these conditions, butterflies were released individually from the boat moored near the centre of Buena Vista bay on Lake Gatún (distance from shoreline approximately 1200 m). Butterflies were not exposed to skylight until release. Control and experimental individuals were released alternately at 2–3 min intervals. For release, each butterfly was placed on the dorsal surface of the releaser's left hand positioned above his head before release. Butterflies voluntarily adopted variable body orientations prior to take-off. After taking off, the butterfly was followed visually, and its vanishing bearing (the compass direction in which the butterfly could no longer be seen with the naked eye) was recorded from the point of release. The individuals disappeared from sight approximately 300–500 m from the point of release. Less than 2% of released individuals landed on the water within approximately 50 m of the site of release. These individuals were excluded from the analysis. All releases were performed by E.G.O. between 10:00 and 11:15 h, and only when the position of the sun was clearly identifiable. Clock-shift releases were performed between 28 May and 20 July over the years 1992–1994.

To estimate the wind conditions each individual experienced following release, we again measured wind direction and wind speed every 2–5 min using a weathervane and an anemometer (TSI, model 1650). Wind direction always refers to the direction of the wind source, except (i) in the vector analysis used to estimate headings and (ii) in Figs 5B,E, 6B,E, 9C, where wind direction refers to wind destination.

To measure the effect of handling on the orientation of butterflies, we conducted an experiment in which migrating butterflies were captured, held in glassine envelopes for 5 min, and released from a point equidistant from both shorelines along the same track each individual was originally flying. Captures and releases were performed between 10:00 and 15:00 h. Wind speed and direction were recorded between the capture and release of each individual.

Data analysis

Primary analysis of orientation data used circular statistics methods as described by Batschelet (1981) with the aid of the software Oriana (Kovach, 1994) and Daten (by A. Ganzhorn). The Rayleigh test was used to test for uniform distribution. Watson's and Watson-Williams' *F*-tests were used for two- and multi-sample comparisons, respectively. These analyses were performed for (i) butterfly track direction before capture, (ii) expected and observed vanishing bearing after treatment, (iii) wind direction at capture and release times, and (iv)

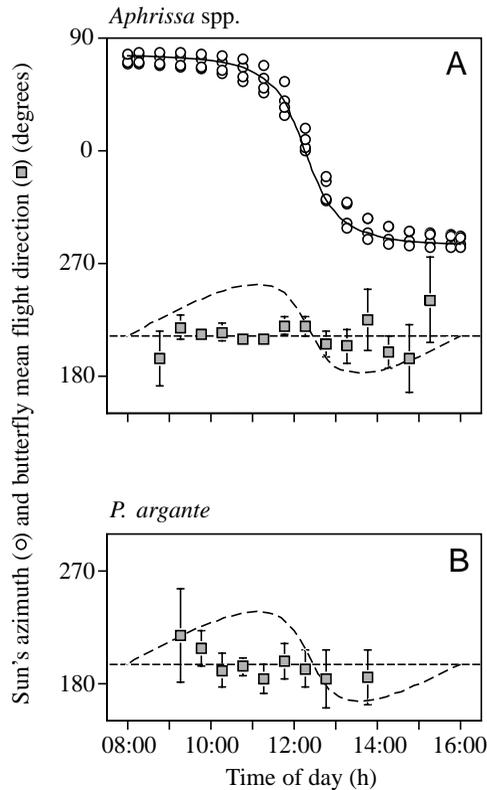


Fig. 4. The sun's azimuth at Barro Colorado Island, Panamá, during the period 10 May to 10 August 1993 (open circles; solid line obtained by interpolation), and track direction of naturally migrating *Aphrissa* spp. (A) and *Phoebis argante* (B) butterflies over Lake Gatún versus time of day (GMT minus 5 h) (filled squares). Mean flight direction and 95% confidence intervals for 30 min periods are plotted (see also Table 1). With full compensation for the sun's movement (and wind speed not exceeding 2 m s^{-1}), the predicted flight direction is the mean flight direction (horizontal broken line). The expected flight direction with compensation based on the mean motion of the sun between 08:00 and 16:00 h (curvilinear dashed line) was estimated as the difference between the sun's true position and its average position. In both species, the confidence intervals for mean flight direction from each 30 min of data overlap the horizontal line but are very different from the curvilinear one.

estimated butterfly heading (i.e. body compass orientation, see below) following release.

For controls, the expected vanishing bearing on release was the flight direction (track) measured prior to capture. For experimental individuals (4 h time shift), on the basis of the sun's azimuth curve for Barro Colorado Island in the period 10 May to 10 August (see Fig. 4A), the expected vanishing bearing on release was the individual's original track direction plus 120° . In 1992, however, the butterfly track direction before capture was not recorded. For all individuals captured in 1992, we used the mean flight direction ϕ obtained from samples of naturally migrating butterflies in that period (*Aphrissa* spp., $\phi = 225 \pm 5^\circ$, $R = 0.758$, $P < 0.0001$, $N = 510$; *P. argante*, $\phi = 190 \pm 10^\circ$, $R = 0.751$, $P < 0.0001$, $N = 89$; mean $\pm 95\%$ CIs; Fig. 2) as the basis for calculating expected bearings.

We used vector analysis to estimate the heading of individual butterflies following release (for methods, see Srygley *et al.* 1996). Individual wind direction and wind speed were the best estimates based on measurements made at 2–5 min intervals; individual vanishing bearings were entered as their track direction; and 4.5 m s^{-1} was set as the butterfly air speed for all individuals (*A. statira* and *P. argante*, controls and experimentals). To account for the observation that released butterflies fly more slowly than those crossing the lake naturally (Dudley and Srygley, 1994), the set air speed was approximately 10% less than the mean air speed measured during natural flight (see Srygley *et al.* 1996).

To analyze the effect of wind direction on the observed vanishing bearings of released butterflies, we regressed the magnitude of the differences between the expected and observed vanishing bearings on the magnitude of the differences between the wind direction and expected vanishing bearings. If wind direction had an effect on the vanishing bearing of released butterflies, the difference between the expected and observed vanishing bearing would increase as the difference between the wind direction and expected vanishing bearing decreased (i.e. as wind direction became more adverse). For *A. statira*, we tested for effects of treatment and wind direction on the difference between the expected and observed vanishing bearings using a two-way analysis of variance (ANOVA). For this test, wind direction was divided into three categories (adverse, cross- or favourable) on the basis of the magnitude of the difference between the wind direction and the expected vanishing bearing. We also used ANOVA to test whether the wind speed experienced by control and experimental butterflies differed among the three wind direction categories. Finally, to verify whether wind speed *per se* had an impact on the flight orientation of released butterflies, we regressed the magnitude of the difference between the expected and observed vanishing bearings on wind speed.

Results

Time of day and flight direction of naturally migrating butterflies

When wind speed did not exceed 2 m s^{-1} , there was no significant effect of time of day t (in h) on the flight direction D (in degrees) of naturally migrating *Aphrissa* spp. ($N = 784$; $D = 196 + 1.64t$; CIs, $-0.43, 3.47$; $P = 0.099$; Fig. 4A). *P. argante* showed a small but significant counter-clockwise change of direction ($N = 135$; $D = 258 - 5.65t$; CIs, $-10.55, -0.75$; $P = 0.024$; Fig. 4B) (Table 1). Since wind speed typically increased with time of day, a large fraction of bearings recorded in the afternoon were excluded from this analysis. When data gathered at all wind speeds were included, both species showed significant changes (*Aphrissa* spp.: $N = 1622$; $D = 191 + 1.67t$; CIs, $0.37, 2.97$; $P = 0.012$; *P. argante*: $N = 279$; $D = 231 - 3.07t$; CIs, $-5.96, -0.19$; $P = 0.037$) (Table 1). However, these changes were still very small. Even when the effects of wind were not controlled for, very little change in flight direction occurred over the course of a day. The estimated rate of

Table 1. *Flight direction of naturally migrating Aphrissa spp. and Phoebis argante butterflies on Lake Gatún, Panamá (May–July 1992–1996)*

Species	Time of day (h)	<i>N</i>	<i>r</i>	ϕ (degrees)	$\pm\delta$ (degrees)	<i>R</i>	<i>P</i>
<i>Aphrissa</i> spp.	08:31–09:00	8 (7)	0.924 (0.918)	196 (194)	20 (23)	7.390 (6.425)	0 (0)
	09:01–09:30	34 (33)	0.862 (0.870)	217 (219)	11 (10)	29.319 (28.716)	0 (0)
	09:31–10:00	93 (69)	0.892 (0.895)	209 (213)	6 (7)	82.927 (61.756)	0 (0)
	10:01–10:30	143 (97)	0.848 (0.839)	213 (215)	6 (7)	121.247 (81.410)	0 (0)
	10:31–11:00	231 (152)	0.878 (0.897)	206 (210)	4 (5)	202.791 (136.278)	0 (0)
	11:01–11:30	287 (155)	0.872 (0.849)	204 (209)	4 (5)	250.225 (131.533)	0 (0)
	11:31–12:00	271 (109)	0.836 (0.812)	210 (220)	4 (7)	226.421 (88.500)	0 (0)
	12:01–12:30	223 (77)	0.861 (0.828)	214 (220)	4 (8)	192.063 (63.759)	0 (0)
	12:31–13:00	137 (28)	0.857 (0.899)	213 (206)	6 (10)	117.429 (25.161)	0 (0)
	13:01–13:30	84 (23)	0.876 (0.855)	212 (204)	7 (13)	73.560 (19.659)	0 (0)
	13:31–14:00	59 (12)	0.869 (0.807)	212 (225)	8 (24)	51.290 (9.688)	0 (0)
	14:01–14:30	28 (6)	0.889 (0.979)	201 (199)	11 (13)	24.898 (5.874)	0 (0)
	14:31–15:00	13 (4)	0.830 (0.956)	209 (194)	22 (27)	10.784 (3.824)	0 (0.014)
	15:01–15:30	8 (8)	0.777 (0.777)	241 (241)	34 (34)	6.218 (6.218)	0.004 (0.004)
	15:31–16:00	3 (3)	0.987 (0.987)	257 (257)	21 (21)	2.960 (2.960)	0.038 (0.038)
<i>Phoebis argante</i>	08:31–09:00	3 (3)	0.722 (0.722)	221 (221)	–	2.166 (2.166)	0.225 (0.225)
	09:01–09:30	7 (7)	0.783 (0.783)	219 (219)	37 (37)	5.480 (5.480)	0.008 (0.008)
	09:31–10:00	24 (20)	0.876 (0.859)	207 (208)	12 (14)	21.017 (17.171)	0 (0)
	10:01–10:30	30 (20)	0.890 (0.883)	191 (191)	10 (13)	26.696 (17.661)	0 (0)
	10:31–11:00	33 (23)	0.948 (0.953)	193 (194)	6 (7)	31.295 (21.908)	0 (0)
	11:01–11:30	47 (26)	0.874 (0.853)	191 (184)	9 (12)	41.100 (22.188)	0 (0)
	11:31–12:00	36 (11)	0.919 (0.937)	194 (198)	8 (14)	33.086 (10.307)	0 (0)
	12:01–12:30	45 (17)	0.851 (0.860)	198 (192)	10 (15)	38.274 (14.622)	0 (0)
	12:31–13:00	25 (5)	0.945 (0.950)	190 (184)	8 (23)	23.619 (4.751)	0 (0.004)
	13:01–13:30	14 (1)	0.733 (1.000)	205 (260)	26 (–)	10.260 (–)	0 (0.512)
	13:31–14:00	7 (2)	0.872 (0.996)	193 (185)	28 (22)	6.101 (1.992)	0.002 (0.140)
	14:01–14:30	4 (1)	0.980 (1.000)	176 (195)	18 (–)	3.922 (–)	0.010 (0.512)
	14:31–15:00	4 (0)	0.962	179	25	3.848	0.013

Number in parentheses are only for those cases when wind speed did not exceed 2 m s⁻¹.

N, sample size; *r*, length of mean vector; ϕ , mean flight direction; δ , angle of deviation from ϕ with a 95% confidence coefficient; *R*, Rayleigh test for uniformity; a dash means no values are available.

directional change in the total data set (all wind speeds) was no higher than the rate in the data set gathered at low wind speeds. This result corroborates our previous finding showing that naturally migrating *A. statira* and *P. argante* compensate to a large extent for cross-wind drift (Srygley *et al.* 1996).

Capture and release times

Captures took place during the whole period of flight activity with mean capture time between 11:30 and 12:00 h in both species. For both species, the two treatments did not differ in mean capture time (time of day that they were captured) (*A. statira*, $t=0.67$; d.f.=159, $P=0.253$; *P. argante*, $t=-0.39$; d.f.=29, $P=0.350$).

The mean release times for *A. statira* in 1992–1994 were 10:36 h \pm 2 min (mean \pm S.E.M.; range 09:59–11:13 h) for controls and 10:37 h \pm 2 min (range 10:01–11:15 h) for experimentals, with no significant difference between the two treatments ($t=-0.443$, d.f.=187, $P=0.659$). On average, releases (controls and experimentals combined) were performed 10–14 min earlier in 1994 than in 1992–1993 ($F_{2,186}=13.695$,

$P<0.0001$; 1992 *versus* 1993, $P=0.828$; 1992 *versus* 1994, $P=0.0002$; 1993 *versus* 1994, $P<0.0001$). This time difference corresponded to a change in the sun's azimuth of less than 4°.

The mean release times for *P. argante* (1992–1994) were 10:50 h \pm 4 min (range 10:16–11:10 h) for controls and 10:50 h \pm 4 min (range 10:16–11:12 h) for experimentals, again with no significant difference between the two groups ($t=-0.008$, d.f.=34, $P=0.994$). On average, releases (controls and experimentals combined) were performed 22–26 min earlier in 1992 than in 1993–1994 ($F_{2,33}=5.888$, $P=0.0065$; 1992 *versus* 1993, $P=0.0031$; 1992 *versus* 1994, $P=0.0035$; 1993 *versus* 1994, $P=0.519$). This time difference corresponded to a change in the sun's azimuth of approximately 5°. On the basis of the mean release time, the difference between the two treatments was predicted to be approximately 2° less for *P. argante* than for *A. statira*.

The effect of clock-shifting

The sun's azimuth curve for the corresponding latitude and time of the year deviates greatly from that plotted for the sun's

mean rate of movement (15°h^{-1}) but remains fairly constant across the season (Fig. 4A). Because releases took place between 10:00 and 11:15 h, one would expect the mean orientation of experimental (4 h advance shift) butterflies to be approximately 120° clockwise relative to that of controls (experimentals should expect the sun to be near 295° rather than near 55°). The mean vanishing bearing of released controls was expected not to differ from the mean flight orientation recorded prior to capture. This ideal 'expected' scenario assumes (i) that the butterflies showed perfect compensation for the sun's apparent movement (i.e. that the butterflies use a fully time-compensated sun compass), (ii) that the treatment produced the expected degree of shift in the endogenous chronometer of butterflies in the experimental group, (iii) that the wind direction and wind speed experienced by each individual were the same at the times of capture and release (since these butterflies are to a certain extent subject to wind drift; Srygley *et al.* 1996), (iv) that the treatment had no

effect on the butterfly's ability to compensate for wind drift (i.e. that flight performance was the same before and after treatment), and (v) that there was no effect of capture, handling or captivity on the butterfly's navigation system (i.e. that preferred migratory bearing was not affected).

The pooled 1992–1994 data for *A. statira* show that, on release, 4 h advance-shifted butterflies oriented significantly differently from their respective controls ($F_{1,189}=43.486$, $P<0.0001$; Fig. 5D). The two groups did not differ in mean flight direction before capture (Fig. 5A). In all three years, the mean vanishing bearing of experimentals was clockwise relative to that of controls. This difference was significant in 1992 ($P<0.002$) and in 1993 ($P<0.0001$) but not in 1994 ($P=0.256$) (Table 2, which also shows across-year comparisons within each group). The 1992–1994 mean vanishing bearings showed a difference of 70° between the two groups (Fig. 5D). Estimated butterfly heading, in contrast, showed a difference of 91° between the two treatments

Table 2. Mean flight direction of control and experimental *Aphrissa statira* and *Phoebis argante* butterflies before capture and when released on Lake Gatún after treatment in the 4 h advance shift experiment

Species	Year	Treatment	Capture/ release	N	r	ϕ (degrees)	$\pm\delta$ (degrees)	R	P
<i>Aphrissa statira</i>	1992	Control	Release	14	0.584	117	34	8.183	0.006
		Experimental	Release	14	0.776	188	24	10.863	0
	1993	Control	Capture	57	0.849	195	9	48.393	0
			Release	57	0.365	110	28	20.811	0.001
		Experimental	Capture	51	0.834	195	10	42.512	0
	1994	Control	Release	51	0.597	209	17	30.465	0
			Capture	26	0.930	207	9	24.182	0
			Release	26	0.700	158	19	18.193	0
		Experimental	Capture	27	0.927	210	9	25.017	0
			Release	27	0.420	180	35	12.125	0.007
Release			27	0.420	180	35	12.125	0.007	
All years	Control	Release	97	0.448	129	17	43.480	0	
	Experimental	Release	92	0.558	199	14	51.326	0	
<i>Phoebis argante</i>	1992	Control	Release	2	0.999	103	11	1.998	0.138
		Experimental	Release	3	0.921	197	51	2.762	0.067
	1993	Control	Capture	4	0.843	203	52	3.371	0.048
			Release	4	0.274	164	-	1.094	0.765
		Experimental	Capture	4	0.831	183	54	3.325	0.053
	1994	Control	Release	4	0.499	101	94	1.997	0.395
			Capture	11	0.955	191	12	10.506	0
		Experimental	Release	11	0.767	110	29	8.433	0.001
			Capture	12	0.935	181	14	11.225	0
			Release	12	0.662	158	31	7.943	0.003
All years	Control	Release	17	0.651	113	26	11.075	0	
	Experimental	Release	19	0.588	158	28	11.180	0.001	

Symbols are as in Table 1.

F, Watson's (two samples) or Watson-Williams' (more than two samples) F-test.

In 1992, the flight direction before capture was not available.

Statistical comparisons are as follows. *A. statira*: 1992 control/release versus experimental/release, $F_{1,26}=12.191$, $P=0.002$; 1993 control/release versus experimental/release, $F_{1,106}=43.312$, $P<0.0001$; 1994 control/release versus experimental/release, $F_{1,51}=1.317$, $P=0.256$; control/release across years, $F_{2,94}=4.865$, $P<0.025$; experimental/release across years, $F_{2,89}=1.972$, $P>0.10$; control/capture (1993 versus 1994), $F_{1,81}=3.087$, $P=0.083$; experimental/capture (1993 versus 1994), $F_{1,76}=4.115$, $P=0.046$. *P. argante*: 1992 control/release versus experimental/release, $F_{1,3}=18.629$, $P=0.023$; 1993 control/release versus experimental/release, $F_{1,6}=1.022$, $P=0.351$; 1994 control/release versus experimental/release, $F_{1,21}=5.459$, $P=0.029$.

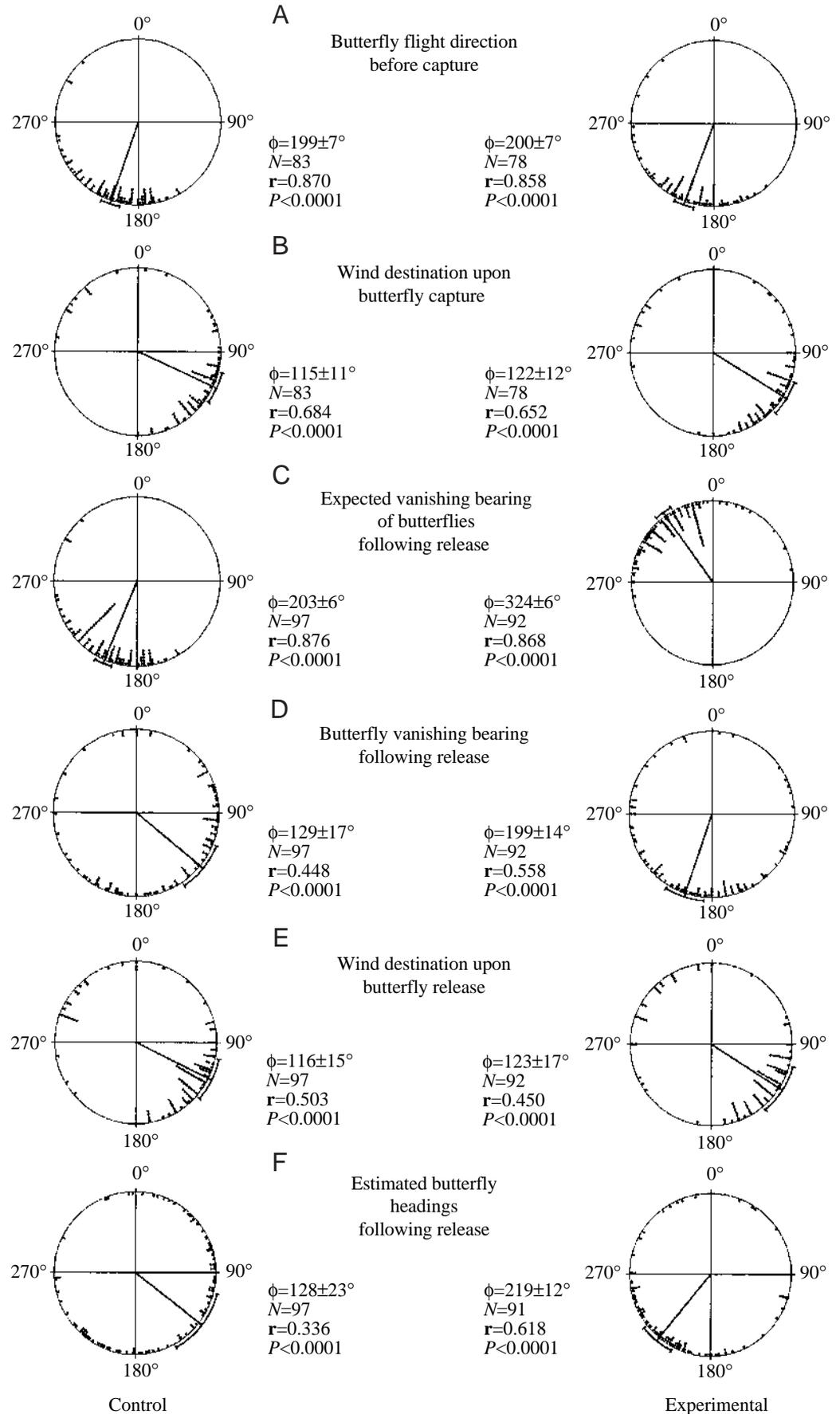


Fig. 5. Orientation of control and experimental *Aphrissa statira* before capture (A) and when released following treatment in the 4h advance shift experiment (D). Also shown is the wind destination at the moment of capture (B) or release (E), the expected vanishing bearing of released butterflies based on the 4h clock shift (C), and the estimated butterfly headings at release (F) calculated from their vanishing bearing, air speed, wind speed and wind direction. Data are for 1992–1994. Small triangles represent individual bearings. An arc outside each circle shows the mean direction with 95% confidence intervals. ϕ , mean direction; N , number of observations; r , length of mean vector; P , significance (Rayleigh test). Among experimentals, there was one case with no single solution for heading, so it was excluded (F).

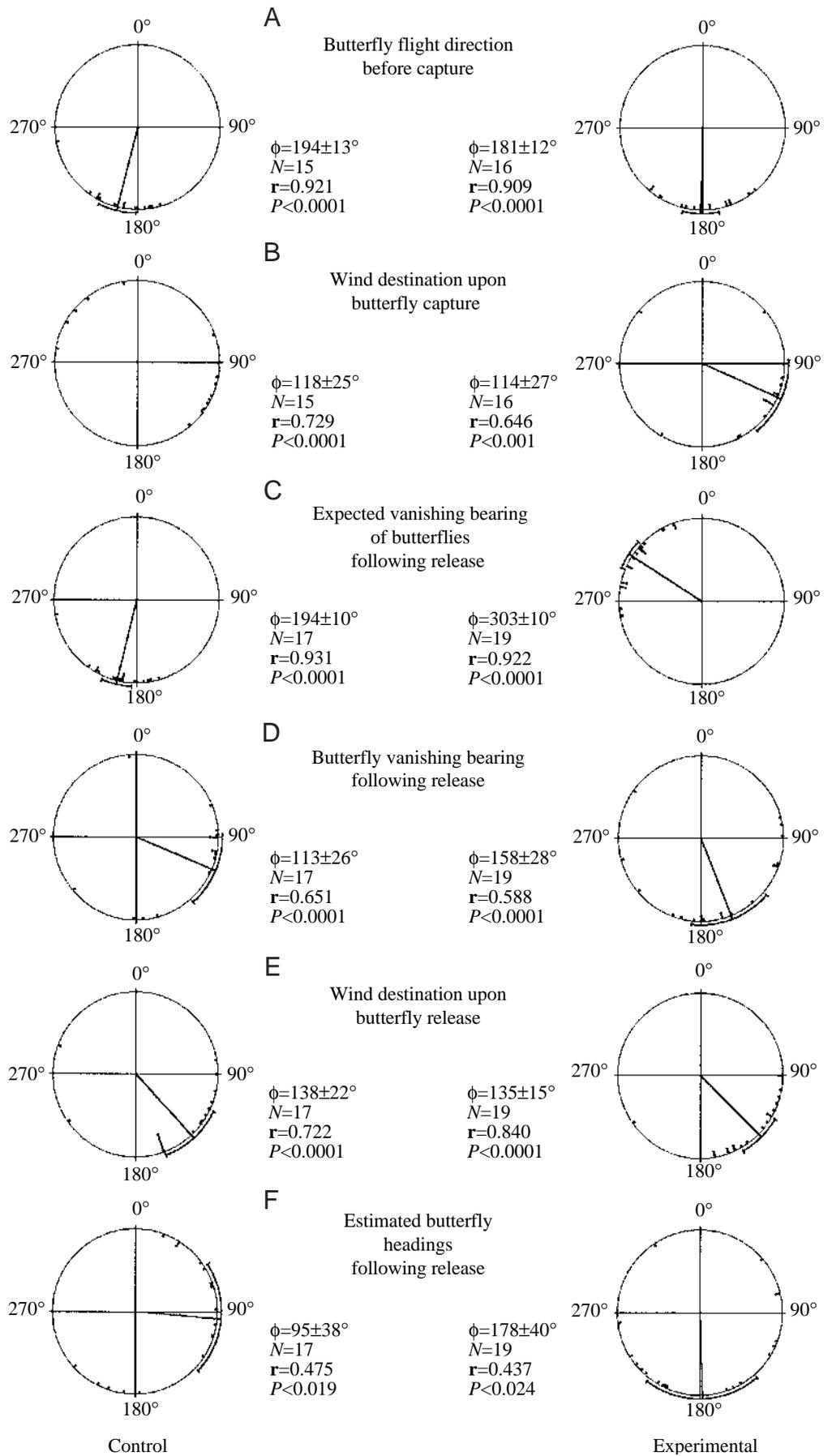


Fig. 6. Orientation of control and experimental *Phoebis argante* before capture (A) and when released following treatment in the 4h advance shift experiment (D). Also shown is the wind destination at the moment of capture (B) or release (E), the expected vanishing bearing of released butterflies based on the 4h clock shift (C), and the estimated butterfly headings at release (F) calculated from their vanishing bearing, air speed, wind speed and wind direction. Data are for 1992–1994. Symbols as in Fig. 5. The mean vector for wind direction before capture of controls (B) was obtained by doubling the angles (Batschelet, 1981, p. 25). The mean vector is not shown because in this case the software (Kovach, 1994) automatically displays the data as axial (i.e. each angle is plotted twice in symmetrically opposite directions).

($P < 0.0001$; Fig. 5F). This latter value corresponds to 76% of the predicted 120° difference between the two treatments. The observed mean vanishing bearings of released controls and experimentals were both shifted counter-clockwise with respect to the predicted direction. The magnitude of this shift was 74° for controls and 125° for experimentals (Fig. 5C,D).

Similar results were obtained for *P. argante*. Upon release, 4h advance-shifted butterflies oriented significantly differently from controls (1992–1994: $F_{1,34}=5.239$, $P=0.028$; Fig. 6D; Table 2). The mean vanishing bearing of experimentals was 45° clockwise relative to that of controls. There was also a non-significant difference of 13° between the two groups before capture ($F_{1,29}=1.923$, $P=0.176$; Fig. 6A). Estimated headings of released butterflies show a difference of 83° between the two treatments (Fig. 6F), corresponding to 69% of the predicted difference (120°). The difference in mean vanishing bearing between the two groups was significant in 1992 ($F_{1,3}=18.629$, $P=0.023$) and 1994 ($F_{1,21}=5.459$, $P=0.029$). In both years, experimentals oriented clockwise with regard to controls (vanishing bearings in 1993 were uniformly distributed in both groups). As with *A. statira*, the mean vanishing bearings of released controls and experimentals were both counter-clockwise with respect to the expected means. This difference was 81° for controls and 145° for experimentals (Fig. 6C,D).

The estimated headings precisely illustrate differences in the flight behaviour exhibited by released control and experimental butterflies. Following release, control butterflies typically flew with the prevailing northwest winds, whereas experimentals appeared to adjust their headings so that they compensated for this cross-wind drift. The behaviour of experimentals resulted in a curvilinear track from the point of release to their vanishing point. Therefore, the difference between the two groups based on the estimated headings, rather than that based on the vanishing bearings, seems to be a more accurate representation of the magnitude of the clock-shifting effect (see also Perez *et al.* 1997).

The effects of wind direction and wind speed

Winds from the northwest (and to a lesser extent from the southeast) prevailed during field work in all three years (Figs 5B,E, 6B,E). Winds were therefore approximately perpendicular to the preferred migratory direction at this time of the year. For *A. statira*, the combined (controls and experimentals) 1992–1994 mean wind direction (source) during releases was $299 \pm 11^\circ$ (mean $\pm 95\%$ CIs; $N=189$, $P < 0.0001$) and there was no effect of year ($F_{2,186}=3.976$, $P > 0.10$). The combined 1992–1994 mean wind speed during releases was $2.3 \pm 0.1 \text{ m s}^{-1}$ (mean \pm S.E.M.; range $0.1\text{--}5.8 \text{ m s}^{-1}$, $N=189$), but there was significant variation across the years ($F_{2,186}=12.341$, $P < 0.0001$), with 1994 winds being relatively stronger (1992 versus 1993, $P=0.992$; 1992 versus 1994, $P=0.0007$; 1993 versus 1994, $P < 0.0001$). This factor may explain the more similar control and experimental mean vectors of released *A. statira* in 1994 (Table 2) (i.e. stronger winds from the northwest would tend to bring the two mean vectors closer).

For *P. argante*, the combined 1992–1994 mean wind

direction (source) on release was $316 \pm 14^\circ$ ($N=36$, $P < 0.0001$), and the mean wind speed was $3.4 \pm 0.2 \text{ m s}^{-1}$ (mean \pm S.E.M.; range $0.1\text{--}6.0 \text{ m s}^{-1}$). Both species encountered the same wind direction on release (control, $F_{1,112}=1.721$, $P=0.192$; experimental, $F_{1,109}=0.551$, $P=0.460$), but *P. argante* experienced higher wind speeds than did *A. statira* (control, $t=-3.76$, d.f.=112, $P=0.0001$; experimental, $t=-3.07$, d.f.=109, $P=0.001$). This factor may explain the smaller difference between mean release vectors for the two treatments in *P. argante* compared with *A. statira* (see Table 2). In both species, controls and experimentals experienced the same wind direction (1992–1994: *A. statira*, $F_{2,187}=1.324$, $P=0.251$; *P. argante*, $F_{1,34}=0.026$, $P=0.873$) and wind speed (1992–1994: *A. statira*, $t=-0.11$, d.f.=187, $P=0.457$; *P. argante*, $t=0.48$,

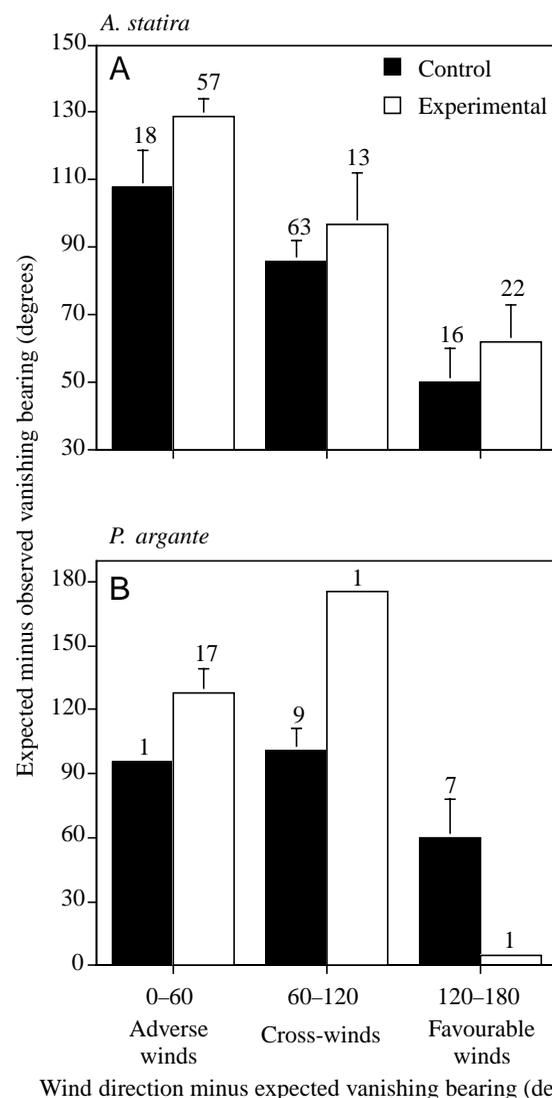


Fig. 7. Mean difference (\pm S.E.M.) between absolute values of expected and observed vanishing bearings for *Aphrissa statira* (A) and *Phoebis argante* (B) in three 60° wind direction categories depending on whether it was favourable, cross or adverse to the expected vanishing bearing of released controls (filled columns) and experimentals (open columns) in the clock-shift experiment. N is given above each column.

d.f.=34, $P=0.317$) on release. For both species, wind direction during release was not significantly different from wind direction during capture (1993–1994: *A. statira*, control, $F_{1,164}=0.022$, $P=0.882$; experimental, $F_{1,154}=0.007$, $P=0.935$; *P. argante*, control, $F_{1,28}=3.162$, $P=0.086$; experimental, $F_{1,30}=1.819$, $P=0.188$). In contrast, wind speed during releases was lower than wind speed during captures for *A. statira* (1993–1994: control, $t=3.42$, d.f.=164, $P<0.0001$; experimental, $t=2.89$, d.f.=154, $P=0.002$) but higher for *P. argante* (control, $t=-2.45$, d.f.=28, $P=0.010$; experimental, $t=-1.97$, d.f.=30, $P=0.029$). This factor may also have contributed to the smaller difference between the mean release vectors of the treatments in *P. argante*.

Wind direction had a strong effect on the vanishing bearing of released butterflies. As the wind direction became more favourable (with respect to the expected vanishing bearing following release), the difference between the expected and the observed mean vanishing bearing decreased (Fig. 7). Linear regression for wind direction minus expected vanishing bearing *versus* expected minus observed vanishing bearing showed a significant effect of wind direction in both treatments and species (*A. statira*, control, $y=-0.50x+128.80$, $r^2=0.17$, $N=97$, $P<0.0001$; experimental, $y=-0.48x+141.08$, $r^2=0.29$, $N=92$, $P<0.0001$; *P. argante*, control, $y=-0.83x+179.37$, $r^2=0.43$, $N=17$, $P<0.0001$; experimental, $y=-0.70x+148.50$, $r^2=0.24$, $N=19$, $P=0.034$). For *A. statira*, two-way ANOVA for the difference between expected and observed vanishing bearing showed a marginally significant effect of treatment ($F_{1,183}=3.807$, $P=0.053$) and a significant effect of wind direction ($F_{2,183}=21.513$, $P<0.0001$), but no interaction between these two factors ($F_{2,183}=0.28$, $P=0.812$). In both species, butterflies in the experimental group were mostly released under adverse wind with respect to the predicted bearing following release, while butterflies in the control group were more frequently exposed to crosswinds (Figs 5–7).

For *A. statira*, ANOVA for wind speed in the three wind direction categories showed no significant effect of treatment ($F_{1,183}=3.315$, $P=0.070$) or wind direction ($F_{2,183}=2.127$, $P=0.122$) but a significant interaction between the two factors ($F_{2,183}=8.320$, $P=0.0003$). In addition to being adverse in direction, the winds encountered by most butterflies in the experimental group were also relatively strong (Fig. 8A). Consistent with these observations, the regression of wind speed on expected minus observed vanishing bearing showed a significant effect of wind speed on the vanishing bearing of *A. statira* experimentals ($y=12.05x+81.02$, $r^2=0.08$, $P=0.005$) but not of controls ($y=-1.12x+86.48$, $r^2=0.00$, $P=0.782$). There was no significant relationship between the two variables for *P. argante* (controls, $y=-7.80x+111.16$, $r^2=0.05$, $N=17$, $P=0.415$; experimentals, $y=5.05x+107.04$, $r^2=0.03$, $N=19$, $P=0.519$). Control and experimental *P. argante* experienced essentially the same wind speed (Fig. 8B).

The effect of handling

Captured *A. statira* and *P. argante* that experienced 5 min of captivity prior to release along their original flight trajectory

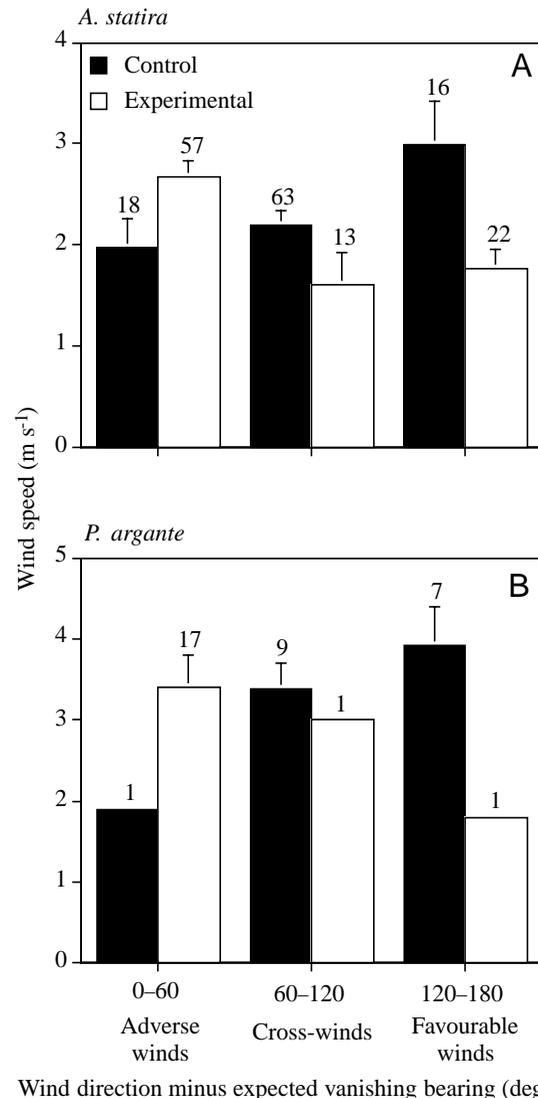


Fig. 8. Mean wind speed (+ S.E.M.) experienced by control (filled columns) and experimental (open columns) *Aphrissa statira* (A) and *Phoebis argante* (B) grouped into the wind direction categories described in Fig. 7.

had a vanishing bearing significantly different from the flight direction measured before capture ($F_{1,72}=32.866$, $P<0.0001$; Fig. 9). This difference can be attributed largely to a tendency of released butterflies to fly with the prevailing winds. Pairwise *t*-tests for *A. statira* showed that the difference between the wind source direction and the butterfly's track direction following release was significantly larger than before capture ($t=-2.783$, d.f.=32, $P=0.005$). Winds from the west-northwest ($293\pm 29^\circ$, $P=0.001$) with a speed of 2.4 ± 0.2 m s⁻¹ (range 0.1–3.9 m s⁻¹) prevailed during such releases. The mean vanishing bearing of *A. statira* subjected to this treatment was not significantly different from that of control butterflies used in the 4 h advance-shift experiment ($F_{1,128}=1.323$, $P=0.252$).

Sex ratio, wing length and body mass

The sex ratio among test individuals was moderately biased

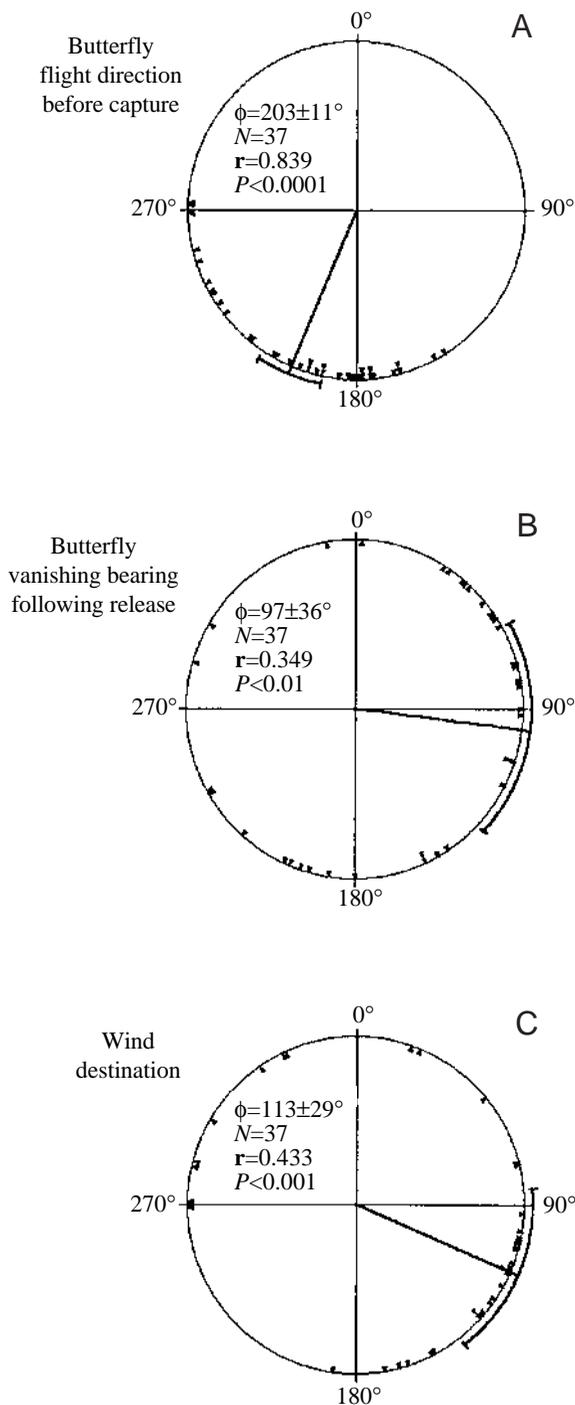


Fig. 9. Orientation of *Aphrissa statira* and *Phoebis argante* before capture (A) (data for both species pooled) and on release 5 min following capture (B). Wind destination is shown in C. Mean vanishing bearings (and 95% CIs) of released butterflies for each species are as follows: *A. statira*, $\phi=108\pm45^\circ$, $N=33$, $P=0.048$; *P. argante*, $\phi=65\pm34^\circ$, $N=4$, $P=0.019$. Other details are as in Fig. 5.

towards males (*A. statira*, control, 1.2:1; experimental, 1:1; *P. argante*, control, 1.4:1; experimental, 2.2:1). There was, however, no significant difference between the control and experimental groups in wing length (*A. statira*, $t=-0.964$,

d.f.=156, $P=0.337$; *P. argante*, $t=-0.700$, d.f.=27, $P=0.490$) or in body mass (*A. statira*, $t=-0.170$, d.f.=156, $P=0.866$; *P. argante*, $t=-1.837$, d.f.=27, $P=0.077$).

Discussion

Taken together, the flight directions of naturally migrating butterflies and those of our experimentally clock-shifted butterflies support the hypothesis that *Aphrissa statira* and *Phoebis argante* use the sun as a compass when migrating. For both species, free-flying butterflies maintained a fairly constant direction throughout the day. Relative to controls, those *A. statira* and *P. argante* with their biological clock experimentally shifted changed their heading in a direction consistent with the use of the sun as a compass (i.e. experimentals oriented clockwise relative to controls). However, the fact that the mean flight direction of the released controls was not the same as that measured prior to capture suggests that these butterflies may use the sun as a compass during escape behaviour. Factors that may have contributed to this change in direction are evaluated below. If this is the case, then by extension to migratory behaviour it is likely that these butterflies also use the sun as a compass when migrating. However, in studies of navigation, such as those with pigeons *Columba livia*, the mean direction of control groups rather than the home direction identifies the reference (Sollwert) for evaluating the effects of clock-shifts (see Wiltschko *et al.* 1994) to incorporate the effects of handling. Similarly, the direction of released controls, rather than the migratory direction, is presumed to be the reference in the present study with butterflies.

Results for both naturally migrating and experimental butterflies support the hypothesis that the butterflies compensate fully for changes in the sun's position over the course of the day. The flight direction of naturally migrating *Aphrissa* spp. did not differ significantly from the mean bearing over the course of a day, while *P. argante* showed only a slight directional change. For both species, the magnitude of the experimental shift in mean estimated heading ($91\pm35^\circ$ for *A. statira* and $83\pm78^\circ$ for *P. argante*) was not significantly different from the expected change of 120° if the butterflies were fully compensating for a shift in the sun's position from 10:00 to 14:00 h. However, it was also not significantly different from the expected change of 60° if the butterflies compensate by time-averaging the sun's change in position over 4 h.

Because the rate of change in the sun's azimuth is not constant over the course of the day (Fig. 4A), the use of the sun as a reliable orientation cue requires a variable time-compensation mechanism (e.g. the use of astronomical tables). In this regard, tropical latitudes provide an extreme environment. At temperate latitudes, compensating by time-averaging the sun's apparent movement over the course of the day and by fully compensating generally give more similar results than at tropical latitudes. Hence, butterflies might opt for time-averaging in temperate latitudes. For *Danaus*

plexippus at a temperate latitude (Kansas, USA), Perez *et al.* (1997) found that estimated headings of 6 h delayed butterflies were shifted in the appropriate direction. The magnitude of the shift (75° relative to controls and 85° relative to the natural flight direction) agreed with that expected from the sun's average rate of azimuthal movement (in which case the predicted shift would be 90°). However, the predicted shift if the butterflies were released in mid-afternoon and were compensating fully was approximately 120°. Hence, the effect of the time-shift was consistent with the time-averaging mechanism and fell short of the full-compensation mechanism.

The effect of experimentally clock-shifting organisms may be less than predicted for a variety of reasons, including duration of treatment, age, direction of shift, incomplete compensation for the sun's movement and conflict with compass information provided by other cues (Aschoff, 1978; Wiltschko *et al.* 1994; Chappell, 1997). In the present study, a reasonable supposition is that treatment duration was less than that required to achieve the desired degree of shift. We opted to keep the treatment duration between 2 and 4 days considering that mortality increased with increasing captivity time. Moreover, if these butterflies in nature undergo continuous migration for only a few days, an extended period of captivity could potentially inhibit behaviour associated with migration. Migration in insects is typically restricted to the premature imaginal phase (Johnson, 1969; but see Spieth *et al.* 1998).

The butterfly compass may also allow only partial compensation for changes in the sun's azimuth. Time of day clearly affected the flight direction of these species during migration across Carajás, Brazil (Oliveira, 1990), and that of short-distance migrant pierids in Europe (Baker, 1968*a,b*, 1969). A sun compass with imperfect time compensation has been observed in crustacean sandhoppers *Talitrus saltator* (Wallraff, 1981), ants *Cataglyphis bicolor* (Wehner, 1984), honeybees *Apis mellifera* (Gould, 1980) and pigeons *Columba livia* (Schmidt-Koenig *et al.* 1991*a*; Wiltschko *et al.* 1994; Chappell, 1997). Desert ants, for example, underestimate high rates of change in the sun's azimuth while overestimating low ones (Wehner, 1984).

In the present study, the effects of the prevailing winds explain in great part both (i) the fact that the mean flight direction of released controls was not the same as that measured prior to capture and (ii) the fact that the magnitude of the difference between the two treatments was smaller (but not significantly so) than predicted. The results of the analyses considering the effect of wind on the flight orientation of released *A. statira* and *P. argante* imply that the prevailing northwest winds caused *both* control and experimental mean vectors to shift counter-clockwise. The experimental group was particularly vulnerable to the effects of the wind because these butterflies faced winds that were generally opposing the expected vanishing bearing. Although naturally migrating butterflies adjusted their headings to compensate for wind drift, at least in part (Srygley *et al.* 1996), captive butterflies may be less motivated or physiologically less capable of compensating

for wind drift. For example, in a sample of 13 species, released butterflies had significantly lower body temperatures than those naturally crossing Lake Gatún (Dudley and Srygley, 1994). *A. statira* and *P. argante* captured during migration showed body temperatures 7.5 ± 0.7 °C (mean \pm S.E.M.; $N=10$) and 8.5 ± 0.4 °C ($N=8$), respectively, above ambient temperature (see methods in Srygley and Chai, 1990), a condition not likely to occur in the test individuals prior to release.

As with released control *A. statira* and *P. argante* butterflies in the clock-shift experiment, a nearly downwind flight was the most obvious effect of capture and handling in the 5 min captivity experiment. Kanz (1977) reported the same effect in *D. plexippus*. This behaviour allows the most rapid escape from a site where danger is imminent. It is intriguing, however, that, despite this escape behaviour, experimental butterflies (flying under the same wind conditions as controls) altered their flight orientation and adopted a bearing that was shifted in the direction predicted by the sun compass hypothesis. Apparently, this presumed 'escape orientation' is under the control of an endogenous clock. This effect was also observed in sandhoppers *T. saltator* (Papi and Pardi, 1963).

If the sun compass is to be used all year round, long-distance migrants may be required to compensate not only for the time of day but also for the seasonal variation in the sun's arc, especially in tropical latitudes. This is difficult to achieve, but some organisms do approach a true solar calendar (e.g. the internal ephemeris function of homing pigeons appears to lag behind real time by several weeks; Schmidt-Koenig *et al.* 1991*b*). The butterflies studied here may circumvent this problem by confining their migratory activity to a period when the sun's course is relatively stable (Figs 1, 4A). In Panamá, major transitions in the sun's course occur in early September and mid April (i.e. from September to April, the midday sun is due south).

Migrating butterflies have also been observed to maintain a constant direction when solar information was unlikely to be available, either because the sun was directly overhead (Larsen, 1991) or because the sky was completely overcast (Schmidt-Koenig, 1985; Gibo, 1986; Walker and Littell, 1994). This suggests the use of a geomagnetic compass. Although such a mechanism has never been demonstrated in migrant butterflies (Wehner, 1984; Brower, 1996; Dingle, 1996), it has been documented in the migratory moths *Noctua pronuba* and *Agrotis exclamationis* (Baker and Mather, 1982; Baker, 1987). It is now well established that animals can use a variety of cues in a flexible manner in order to orient and navigate under changeable ambient conditions (Dingle, 1996; Wehner *et al.* 1996).

Butterflies observed migrating across the isthmus of Panamá are probably long-distance travellers (Srygley *et al.* 1996). Butterflies were observed flying in a straight line over the Caribbean Sea beyond visible landmarks off the northern Colombian coast, and the direction of flight was the same as that observed in central Panamá (R. B. Srygley and E. G. Oliveira, unpublished data). To orient reliably, the use of a time-compensated sun compass may be crucial for these

neotropical migrants. In addition to being essential to our understanding of the ecology and evolution of migration, research on the orientation mechanisms used by migratory butterflies may contribute to the preservation of these spectacular natural phenomena. Their ability to keep within a flyway in variable topographical and wind conditions requires reliable cues for orienting and navigating (Srygley *et al.* 1996). The sun provides such a cue, and the butterflies have adapted to compensate for its motion so as to maintain a constant bearing through the day. As habitat loss narrows corridors that are suitable to sustain long-distance migrations, knowledge of the ability of butterflies to orient and navigate is pertinent to mapping migration flyways and ultimately to conserving migrations (Brower and Malcom, 1991).

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