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Orientation of Fall-migrating Butterflies in North Peninsular Florida and Source Areas

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Abstract

Phoebis sennae (Pieridae), *Agraulis vanillae* (Heliconidae) and *Urbanus proteus* (Hesperiidae) migrate into peninsular Florida each fall from summer breeding areas throughout the south-eastern United States. Fall flight directions of the three species were studied at 78 sites for clues to their means of orientation and migratory routes. Mean flight directions for a visit to a site were calculated using conventional circular statistics. The distribution of flight directions permitted using linear procedures to combine visit means. The overall mean direction (OMD) of a species at a site was defined as the mean of visit means, weighted by frequency/angular variance, with a lower limit of 0.2 imposed on angular variance. In intensive studies at two sites at Gainesville, Florida, mean flight directions during fall migration were largely independent of time of day and crosswinds. The OMDs of the three species at the two Gainesville sites were similar (142 to 156 °) and not significantly different among species at a site or, for the same group of dates, between sites for a species. However, day-to-day variation among species and between sites was not concordant. Visits to 65 sites on a grid throughout the south-eastern United States and to 11 sites along transects inland from the Gulf and Atlantic coasts yielded 10 cases of a *P. sennae* OMD at a grid or transect site differing significantly from its OMD at the main Gainesville site. In each of these, the OMD was more easterly at sites inland from the Gulf coast or more southerly or south-westerly at sites inland from the Atlantic coast. By unknown means and with large, unexplained day-to-day variations in directions, *P. sennae* converge on peninsular Florida from widespread summer breeding grounds. They do this without closely following the Atlantic or Gulf coasts.

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Introduction

At localities in many parts of the world, large numbers of one or more species of butterfly sometimes fly in straight lines in approximately the same direction

(WILLIAMS 1930). These unidirectional flights, termed 'migrations', often last for days or weeks and may be associated with individuals emigrating from crowded or unfavourable areas or immigrating to seasonally suitable habitats. Because butterflies usually fly near the ground and are easy to identify on the wing, their migrations are easily studied. Nonetheless, in no case has the means of orientation been demonstrated, nor, in the few species in which migrants are known to converge on a known destination, has the means of pathfinding been determined. Few workers have quantified flight directions more specifically than compass points – noteworthy exceptions being SCHMIDT-KOENIG (1979, 1985), WALKER (1985), GIBO (1986) and OLIVEIRA (1990). Our study had two objectives. The first was to describe and analyse variations in migratory directions. This was implemented by intensively recording fall migratory directions at two focal sites in north peninsular Florida. The second was to test the hypothesis that three common migrants in the south-eastern United States converge on peninsular Florida. This was implemented by recording fall migratory directions of these species at sites that were upstream to the directions at the focal sites. Both objectives required that we develop statistical techniques for combining mean migratory directions across sampling dates at a site and for comparing such combined mean directions across sites.

Each fall at least five species of butterflies migrate southward from summer breeding areas in eastern North America that are unfavourable for winter survival. Occupying relatively limited overwintering areas, the butterflies diapause or continue to reproduce. Each spring the fall migrants, or their descendants, migrate northward to reoccupy the extensive breeding areas they abandoned the year before. One of these species, the monarch butterfly, *Danaus plexippus* (Danaidae), is well known (MALCOLM & ZALUCKI 1993). Its abundant fall migrants ride thermals upward and take advantage of favourable winds at high altitudes as they make their ways to a few hibernating sites in the mountains of central Mexico (GIBO 1986). In spring the same individuals return northward to summer breeding areas. The other four species, *Phoebis sennae* (Pieridae), *Agraulis vanillae* (Heliconidae), *Precis coenia* (Nymphalidae) and *Urbanus proteus* (Hesperiidae), are less well known. They migrate through north peninsular Florida southward each fall and northward each spring. Their fall numbers approximate the number of monarchs migrating into Mexico (WALKER 1991; LENCZEWSKI 1992). Most important for this study, they, unlike *D. plexippus*, generally migrate within 3 m of the ground, making it easy to determine their migratory tracks (WALKER 1985).

Summer breeding occurs regularly at least as far north as Arkansas and South Carolina. To get from such widely separated areas to peninsular Florida each fall, migrants must have more than a single compass setting – by some means they must choose migratory directions appropriate to their destination. Previous observations of fall migrants of these four species in north peninsular Florida revealed that most fly approximately south-eastward and parallel to the axis of the peninsula (WALKER 1985). A pilot study of directions of fall migrants north of Gainesville refuted the hypothesis that seemed most likely at the time, that migrants throughout the South-east flew south-eastward until they reached the Gulf or Atlantic

coasts and then followed the coast into peninsular Florida (WALKER 1985). These initial results stimulated the more intensive observations of fall migrations reported here. Studies at Gainesville tested for observer bias and effects of crosswinds, time of day, species, time of season, year, and local site on migratory tracks. Studies in putative source areas throughout the south-eastern United States were designed to detect a pattern in migratory directions from which migratory routes could be deduced.

General Methods

Distinguishing Migrants

A migrating butterfly, unlike one that is feeding, ovipositing, or defending a territory, flies in a straight line with noteworthy persistence. When it comes to an obstacle, such as a dense wood or tall building, it flies up and over rather than deviate to the right or left. If it strikes a barrier under a transparent roof, it continues to fly between the barrier and the roof rather than reversing directions – a behavior that has facilitated development of flight traps to sample butterfly migrations (WALKER 1991; LENCZEWSKI 1992; WALKER & WHITESELL 1994).

Observation Sites

Migrants best reveal their migratory directions when flying across areas free of obstacles and flowers. At Gainesville, two sites, 18 km apart, were used. GVW (Gainesville west, 29 °41.1′N, 82 °29.7′W) was the same 8-ha Bahia grass field used in previous studies (WALKER 1985). GVE (Gainesville east, 29 °39.5′N, 82 °18.5′W) was a closely mowed, 5-ha soccer field. Elsewhere, sites were selected to approximate the nodes of a 100 × 100-km grid, with the exact sites determined by major roadways and publicly accessible, large grassy areas – such as athletic fields, church yards and hay fields. At a few localities, the originally selected observation area proved inaccessible or undesirable on a subsequent visit. In such instances, a replacement observation area was found, as near the first as possible. If the replacement site was >8 km from its predecessor, it was classified as a new site. To augment the grid, 11 sites were established at intervals of 8 to 63 km along two transects that started near a coast and ran perpendicularly inland.

Measuring and Recording Azimuths

To qualify for measurement, a butterfly had to be flying steadily in approximately a straight line and it had to be close enough for the observer to reach its path in time to measure its azimuth as it receded into the distance. Bias in selecting individuals to measure was eliminated by scanning to the left and right and running or walking to the path of the nearest qualifying butterfly.

A Suunto KB-14 sighting compass was used to measure the azimuth of the selected butterfly. As the butterfly was tracked, the compass reading stabilized. The reading was then recorded and the next migrant to be measured was sought. If the butterfly changed its direction sharply (>10 °) and intermittent crosswinds were absent, the butterfly was disqualified and its azimuth not recorded. If the azimuth did not stabilize yet the butterfly remained qualified, the azimuth was recorded when the butterfly disappeared from sight or reached an obstacle that might deflect it.

On each azimuth data sheet was recorded site, observer, temperature, magnetic declination (to convert magnetic bearings to true bearings), and time correction (to convert civil time to local mean time [LMT]). Entries for each azimuth record were civil time, species, azimuth to the nearest degree (clockwise from north), percentage of sky free of clouds (to nearest 10 %), visibility of the sun (unobstructed, disc evident but shielded by haze, etc.), wind direction to the nearest of the eight cardinal compass points (as indicated by a 25-cm ribbon hanging freely at 1 m), wind speed at 1.5 m (to nearest m/s; measured with a hand-held Dwyer pithball anemometer), and notes (anything noteworthy not recorded elsewhere).

The number of azimuths taken during a visit to a site varied with the density of migrants and the
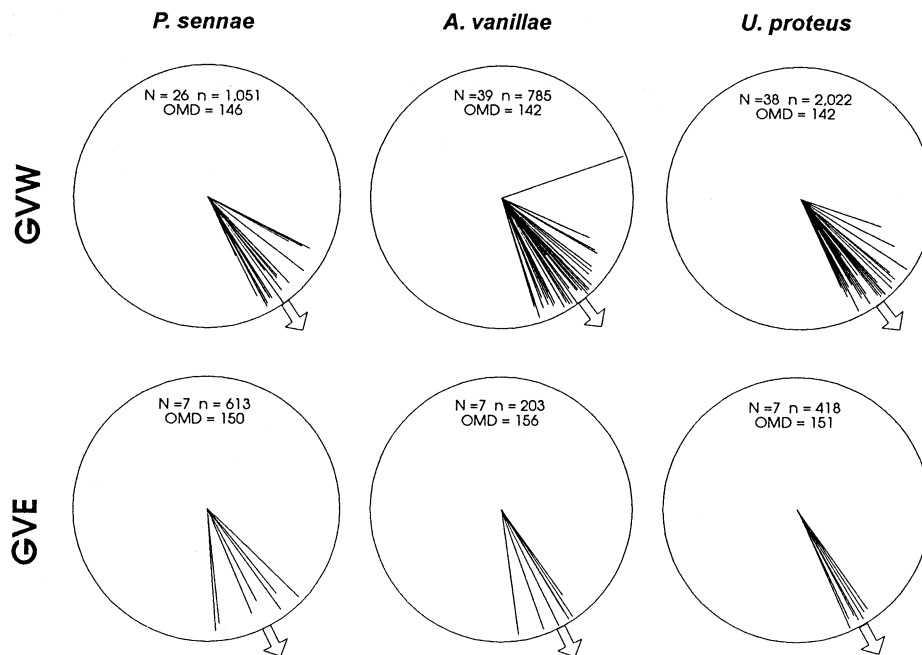
Fig. 1: Mean direction and length of mean vector (r) for all dates when five or more directions were recorded and r exceeded 0.50 for *P. sennae* (left), *A. vanillae* (centre) and *U. proteus* (right). Upper row = Gainesville west; lower row = Gainesville east; N = number of visits portrayed; n = number of records (all visits); OMD = overall mean direction (see text). Arrow external to circle shows OMD

duration of the stay. Stays were prolonged to maximize the number of records for the visit or to get a representative sample of directions when migration was sparse. The briefest stays were 30 min, when no migrants were seen, or 1 h, when migration was dense and other sites were to be visited the same day.

Analysis of Azimuth Records

A substantial body of statistical literature is devoted to the theory and methods of analysing circular data, including books by MARDIA (1972), BATSCHELET (1981) and FISHER (1993). Even so, statistical methods exist only for relatively simply structured data sets. ANOVA methods developed by STEPHENS (1982), HARRISON et al. (1986) and HARRISON & KANJI (1988) extend the Watson–Williams test for one-way classifications to more complex balanced data structures but not to unbalanced cross classifications of directional data. Therefore, in some circumstances, as explained and justified below, we adapted linear and other methods to circular data in novel ways.

All records of fall migration were entered into a computerized database. Subsets of records (generally defined by species, date and site) were analysed to test specific hypotheses about flight directions of migrating butterflies. The database included azimuths for all species that were migrating, but 97 % of the records were for *P. sennae*, *A. vanillae* and *U. proteus*, the three species analysed in this paper.

For each visit to a site, these basic statistics were calculated for each species using conventional methods for circular distributions (BATSCHELET 1981): number of records (freq), mean direction (MD), length of mean vector (r), angular variance (angvar[$= 2 \times (1 - r)$]). Overall mean direction (OMD) for a species at a site was calculated by weighting MDs by freq/angvar and combining them using
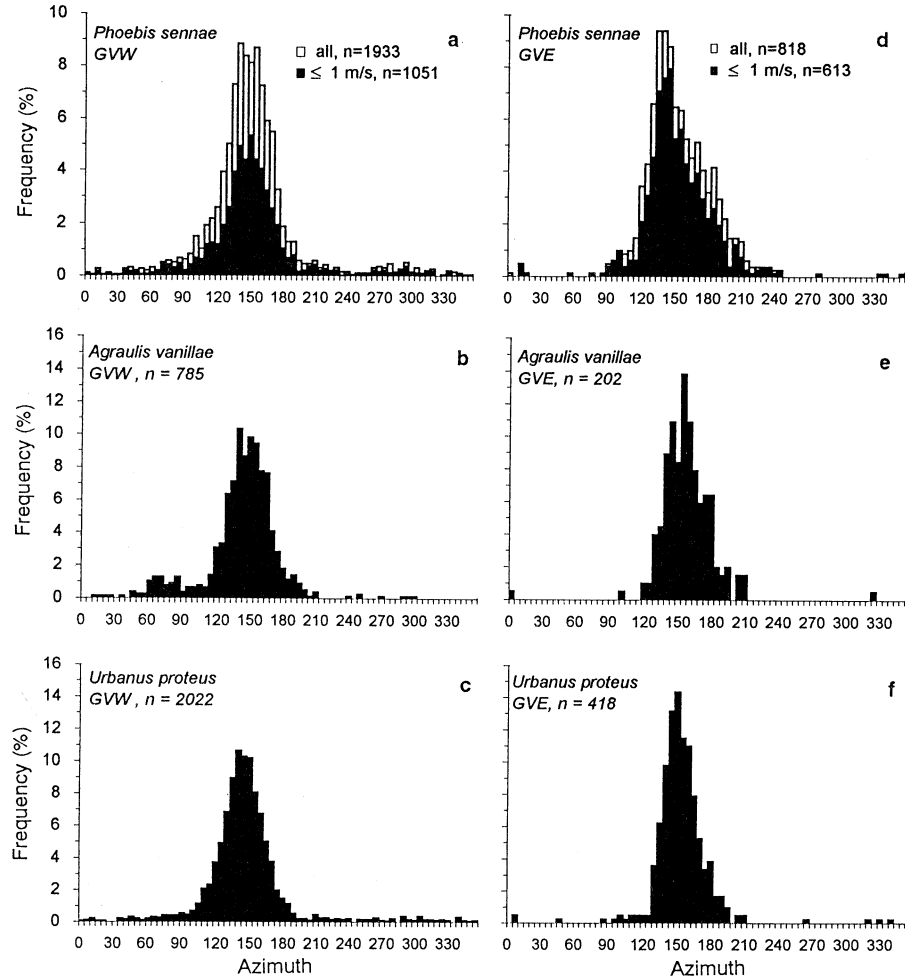
Fig. 2: Histograms of migratory directions recorded at two Gainesville sites, GVW (a–c) and GVE (d–f) for *P. sennae* (a & d), *A. vanillae* (b & e) and *U. proteus* (c & f). *P. sennae* records with wind speed > 1 m/s are indicated by the open portions of the bars

linear statistics. Linear statistical methods, which are appropriate for normally distributed data, can lead to erroneous conclusions when applied directly to directional data. However, in this study linear methods were appropriate to apply to mean directions because (1) MDs at a site fell within a limited range, typically <90 ° (Figs 1, 2), and (2) MDs are approximately normally distributed (MARDIA 1972, p. 110). Freq/angvar was used as a weighting factor to approximate freq/variance, which would be appropriate for normally distributed data. Because unusually small values of angvar, often associated with small samples, gave unduly large weight to their MDs, freq/0.2 was used as the weighting factor whenever angvar was <0.2, i.e. whenever r was >0.90.

Three general types of statistical methodologies were used to compare groups of azimuth records: 1. Watson–Williams test for homogeneity of a set of MDs: F values and degrees of freedom from such tests were used to calculate p-values to assess the statistical significance of differences between the

MDs; 2. Weighted analysis of variance (ANOVA) applied to the MDs via the GLM procedure of the SAS System (SAS INSTITUTE 1988) to compare MDs whenever the Watson–Williams test was not appropriate. This is the case, for example, when testing for the effect of a factor while controlling for effects of another factor by using it as a blocking factor, and the numbers of records are not the same in all groups. ANOVA procedures, which are linear methods, are justified for reasons stated above; 3. Fisher's method of combining independent tests to assess combined significance of effects of a factor from a series of Watson–Williams tests for effects of the factor. In some cases conclusions from the combined tests were combined again with conclusions of an ANOVA test for effect of the factor taking the individual series as blocks.

Additional methods are explained below as components of this study are described and discussed.

Azimuths at Gainesville

A major goal of observations at the two Gainesville sites was to establish a basis for interpreting scantier observations at numerous, more remote sites. The Gainesville data included 6179 records, 2282 of which were previously reported but not fully analysed (WALKER 1985).

Observer Effects

For some of the studies reported here, different observers were used simultaneously or sequentially. It was therefore essential to test for effects of the observer on estimates of mean directions of migrants.

Methods. On seven occasions at peak migration times during 3 yr, two or, in one instance, three observers took azimuths simultaneously at the same Gainesville site. Each observer was assigned a section of the site, and every 30 min observers changed sections. Observations lasted 1 to 2 h with the total records per trial ranging from 104 to 382. The seven trials included five observers in five combinations. Of the 1500 records, 773 were of *P. sennae*, 247 were *A. vanillae* and 480 were *U. proteus*. The five observers individually accounted for 545 (tw), 421 (pc), 239 (ja), 175 (sw), and 120 (dn) records. The Watson–Williams test was used to test for observer effect for each species during each visit. Results from tests during different visits were subjected, by species, to ANOVA with the classes being the five observers and with the data blocked by date (=visit).

Results. The hypothesis of no observer effect was rejected in 1 of 21 Watson–Williams tests. However, when the results for the three species for that visit were combined, the overall probability of observer effect was >0.10 and <0.25. ANOVA probabilities for chance observer effects as great as those measured were 0.73, 0.74 and 0.46 for *P. sennae*, *A. vanillae* and *U. proteus*. Thus, no observer effect was demonstrated.

Discussion. No test was available to determine how large an observer effect might have existed and likely gone undetected in the combined analysis of the seven trials. Observer bias is perhaps most likely for *U. proteus*, because it is the fastest flier and disappears in the shortest distance, giving the observer only about 3 s to establish an azimuth. Indeed, *U. proteus* was the species that had the positive Watson–Williams test; however, the ANOVA combining the records of *U. proteus* for all observer tests yielded p = 0.46.

Table 1: Overall mean directions of migrants at sites with three or more visits for which five or more azimuths were recorded for the species. Sites east of GVW are listed first (results for transect sites in Table 6)

Site	P. sennae $\bar{x} \pm SE$	A. vanillae $\bar{x} \pm SE$	U. proteus $\bar{x} \pm SE$
East of Gainesville			
JXB (S. Carolina)	215 ± 11.6[1]		
HDV (S. Carolina)	153 ± 10.2		
LYN (Georgia)	142 ± 16.1	144 ± 8.4	
BKR (Georgia)			146 ± 9.9
STK (Georgia)		149 ± 9.3	150 ± 6.9
JAX (Florida)	165 ± 9.0[1]	171 ± 6.4[1]	169 ± 5.9[1]
GVE	150 ± 3.7	156 ± 3.2[1]	151 ± 2.5[1]
GVW	146 ± 3.2	142 ± 1.7	142 ± 1.3
West of Gainesville			
SAS (Georgia)	162 ± 18.1		
LVO (Florida)	129 ± 8.0[1]	149 ± 7.0	
OTC (Florida)	148 ± 12.1		
MTC (Florida)	135 ± 11.0		136 ± 5.0
LLD (Florida)	135 ± 7.4		144 ± 9.1
FNL (Florida)	88 ± 12.1[1]		
MRN (Florida)	146 ± 8.8	143 ± 6.1	
DFS (Florida)	120 ± 7.9[1]		141 ± 9.4
MLT (Florida)	113 ± 19.4	129 ± 10.8	
GLN (Alabama)	150 ± 12.7		
MTG (Alabama)	142 ± 9.6		
EUF (Alabama)	156 ± 10.8		
SMS (Alabama)	121 ± 32.6		
DYB (Tennessee)	152 ± 12.6		
HTB (Mississippi)	168 ± 14.3		

[1] Significantly different from overall mean direction at GVW (p ≤ 0.05)

Effects of Crosswinds

Although numbers of fall migrants are greatest on days with no or light wind, migration does not cease until winds exceed 4 or 5 m/s. Unless migrants change their headings to correct for crosswinds, their migratory paths should change, and this could bias analyses of effects of other factors on migratory directions. In intermittent crosswinds, migrants sometimes seem to be blown to the right or left and sometimes seem to correct for the deviation and return to their former tracks. In more constant crosswinds, migrants often maintain headings that appear to compensate for the effect of the crosswind, e.g. a left-shifted heading compensates for a left crosswind.

Methods. To study the effect of crosswinds on migratory directions, the 4740 records from GVW were classified as having right, null or left crosswinds based on the usual direction of migration at GVW being approximately SE (Table 1).

Table 2:   Effects of crosswinds on mean migratory directions of *Phoebis sennae* and *Urbanus proteus* at site GVW. Mean azimuths in the same row that have the same letters are not significantly different (ANOVA, least-square means; p = 0.05)

| Species | Crosswind speed | Type of crosswind | | | Estimated correction | |
		Left	None	Right	Left crosswind	Right crosswind
P. sennae	All	147.9[a]	140.7[b]	134.8[b]	−7.2	+5.9
	≥2 m/s	147.5[a]	141.5[a]	130.7[b]	−6.0	+8.4
U. proteus	All	139.1[a]	143.3[ab]	147.7[b]	+4.2	−4.4
	≥2 m/s	139.3[a]	143.6[ab]	147.9[b]	+4.3	−4.3

Thus wind from N, NE or E was a left crosswind; wind from S, SW or W was a right crosswind; and no wind or wind from NW or SE was a null crosswind. For each species about 40 % of the records lacked crosswinds, 44 % had left crosswinds, and 16 % had right ones. ANOVAs, by species and controlled for date, were used to test the null hypothesis that mean migratory direction was the same regardless of crosswind (i.e. right, left or null). Dividing the records for each date into three categories often left one or two categories with few records and unrealistically low estimates of angular variance. For this reason, records were weighted only by freq (rather than by freq/angvar). Additional ANOVAs were run to test for the effect of crosswinds of different velocities.

Results. Crosswinds had a significant effect on the mean directions of *P. sennae* (1933 records; p = 0.01) but not on those of *A. vanillae* and *U. proteus* (785 and 2022 records; p = 0.26 and 0.07). Crosswinds of 1 m/s did not significantly affect directions of *P. sennae* (482 records, p = 0.10) but crosswinds of 2 m/s or higher did (674 records, p = 0.01).

Discussion. Several factors make the effects of wind on migratory tracks difficult to determine. Wind direction and speed are not easily measured and they generally vary during the time and over the distance that a migrant travels as its azimuth is being taken. The methods of measuring wind used in this study, combined with wind variability in time and space, justified assigning winds to one of no more than eight directions (N, NE, E, . . .) and five speeds (0, 1, . . . 4 m/s). Furthermore, the effect of a given crosswind should be different depending on the exact velocity of the crosswind and angle relative to the heading of the migrant. Finally, most dates did not have a representative sample of crosswinds; indeed, many dates lacked one or two of the three categories.

The fact that migrants often flew with headings that would compensate for drift from concurrent crosswinds suggests that migrants may maintain or approximate their preferred direction in a variety of winds. Indeed, the analyses showed no effects of crosswinds on the tracks of *A. vanillae* or *U. proteus*. The former flies lower than the other migrants (WALKER 1985), usually below 1 m, where winds are lighter than at 1.5 m where wind speed was measured. *U. proteus* almost met the criterion for being judged affected (p = 0.068), but its deviations

Table 3:   Effects of time of day on migratory directions at sites GVW and GVE – slopes of regressions of azimuths on LMT and probabilities that slope = 0 (random coefficient model). Slopes in the same row that have the same letters are not significantly different (ANOVA, p = 0.05). Units for slope are degrees/h

	GVW (Gainesville west)			GVE (Gainesville east)		
Species	n	Slope	Prob.	n	Slope	Prob.
P. sennae	1051	−2.06[a]	0.016	613	1.28[b]	0.192
A. vanillae	785	−0.80[a]	0.348	202	−2.02[a]	0.126
U. proteus	2033	−0.71[a]	0.048	418	−0.34[a]	0.856

for left and right crosswinds had signs opposite to those expected – as though migrants were overcompensating (Table 2).

Including *P. sennae* records with crosswinds >1 m/s could bias analyses of effects of other factors on migratory directions. Applying a correction factor to these *P. sennae* records (e.g. −6 for left crosswinds >1 m/s) is complicated by inaccuracies in measuring wind speed and direction, by the crudeness of the classification of crosswinds, and by variations in mean migratory directions in the absence of crosswinds. Consequently, the risk of bias from not correcting and the risk of making matters worse by trying to correct were both avoided by omitting records for *P. sennae* at winds >1 m/s. This reduced the number of *P. sennae* records for GVW from 1933 to 1051 and for GVE from 818 to 613 (Fig. 2).

Time-of-day Effects

Because visits to sites usually lasted no more than 1 to 2 h during the daily migration period of about 7 h and because successive visits to a site were often at different times of day, it was important to determine whether migratory direction at a site was a function of time of day. Preliminary tests at GVW, based on six dates and reported previously (WALKER 1985), showed no temporal trends for *A. vanillae* and *U. proteus*, but morning and midday directions of *P. sennae* seemed more southerly than afternoon directions.

Methods. During 1982–89, azimuths were taken of fall migrants at GVW during 45 d, with visits lasting from 1 h to all day. During 1987 and 1989, azimuths were taken at GVE on 7 d, with visits lasting from 1.5 to 5 h. For each species and site, azimuths were regressed on LMT and a random coefficient regression model was used to test the hypothesis that the regression coefficient was 0 (GUMPERTZ & PANTULA 1989). ANOVA, by species, was used to test the hypothesis that the regression coefficients at GVW and GVE were equal.

Individuals that were not part of the main migration were excluded from the regression by omitting azimuths that were more than 90° from the mean direction for the visit. This had the effect of excluding records near 0 and 360°, which could have skewed the regression because azimuths rather than rectangular coordinates were regressed. The records omitted amounted to 4.6 % of the *P. sennae* records, 1.7 % of the *A. vanillae* records and 4.1 % of the *U. proteus* records.

Results. The random coefficient analysis showed significant slopes for the

regression of *P. sennae* and *U. proteus* at GVW (p = 0.016 and 0.048), but not for the other four site–species combinations (Table 3). ANOVA showed that regression slopes differed between GVW and GVE for *P. sennae* (p = 0.012), but not for *A. vanillae* and *U. proteus* (p = 0.45 and 0.78).

Discussion. No time-of-day effect was consistent for a species or for a site. *P. sennae* at GVW had the greatest slope (−2.06 °/h), but the same species had a positive and significantly different slope at GVE (+1.28 °/h). Lacking a sizeable and dependable effect of LMT on azimuth, we chose not to correct azimuths for time-of-day effects.

BAKER (1978, 1984) reported that *Pieris rapae* in England varied its rectilinear flight directions with time of day in a manner indicating that each individual flies at a fixed angle to the sun with its angle remaining the same throughout the day. In other words, an individual's azimuth changes ≈+ 15 °/h. BAKER noted that such a non-time-compensated sun compass would facilitate finding new habitat, because areas would not be traversed twice, but would result in a shorter start-to-finish distance than flying for the same duration in a single direction. The behaviour of the three species in the present study suggests they are maximizing distance travelled.

OLIVEIRA (1990) reported that the mean direction of *Phoebis statira* in Pará, Brazil, followed the sun's azimuth in the morning, showed a rapid, reverse change around noon and remained fairly constant in the afternoon. To use BAKER's perspective, *P. statira* behaves as if it were searching for local new habitats in the morning and at noon decides it should cover as much distance as possible for the remainder of the day.

Species Effects

From the above discussion, it is clear that different butterfly species, even if closely related, may behave differently during their migrations. Although our three species of migrants seem to agree in maximizing distance travelled, they could have different destinations to the south that might be reflected in different migratory directions through Gainesville.

Methods. ANOVA was used to test the hypothesis that the three species, at a site, had the same overall mean migratory directions. Data were blocked by date to eliminate possible effects of different proportions of the species on different dates. Watson–Williams tests were used to test for among-species differences on days with at least 10 records, at a site, for each species. This restriction selected days with sufficient numbers of each species to yield usefully precise mean directions for the three species for that site and day – 17 d at GVW and 7 d at GVE. Watson–Williams tests were combined across days to test the hypothesis that the three species had the same mean directions, at a site, each day. ANOVA, not blocked by date, was used to estimate the OMD of each species independent of the other two.

Results. ANOVA showed no significant differences in OMDs of the three migrants at GVW or at GVE (p = 0.82 and 0.72). However, the Watson–Williams tests showed that on 3 of the 17 dates analysed for GVW and on 3 of the 7 d

analysed for GVE, migratory directions differed significantly among the three species. When probabilities from the Watson–Williams tests were combined, at either site, the resultant probability (that the migrants at a site flew the same directions each day) was <0.001. Independent OMD ± SEs for *P. sennae*, *A. vanillae* and *U. proteus* were 146 ± 1.8, 142 ± 1.9 and 142 ± 1.2 at GVW. At GVE they were 150 ± 3.8, 156 ± 6.3 and 151 ± 4.3.

Discussion. The overall mean directions of the three species at a site were the same, as might be expected if each was adapted to fly directly down the Florida peninsula. Yet the mean directions taken by migrants varied from day to day and these variations about the overall mean directions were not concordant. Indirectly, this indicates a species × date interaction. Conceptually, the effects of species, date and interaction could be assessed using ANOVA with sources of variation being species, date, species × date, and error. However, the error term would be computed based on the individual flight directions, which could be invalid due to problems inherent with circular data.

The three species, belonging to different families, are not closely related and must have evolved their migratory directions independently. Their similar OMDs through Gainesville suggest that their destinations lie along the same line.

Date-to-date Variation

The analysis for species effects and Fig. 1 suggest that mean migratory directions for a species at a site may differ significantly from date to date.

Methods. To test for significant date-to-date variation for a species at a site, we ran six Watson–Williams tests (3 spp × 2 sites), using all visits with 10 or more records for the species – n = 23, 25 and 35 at GVW for *P. sennae*, *A. vanillae* and *U. proteus*, and n = 7 for each at GVE.

Results. Five of the six tests showed significant heterogeneity in directions (p < 0.05), the exception being *U. proteus* at GVE (p = 0.16).

Discussion. The results of the species-effects tests (previous section) demonstrated that the causes of date-to-date variation in mean direction differ among the species or at least do not affect the three species the same and synchronously.

Seasonal Effects

Perhaps in addition to erratic date-to-date variation, mean migratory directions change in some regular fashion during each fall.

Methods. The only systematic observations made of variation as a function of season were at GVW in 1983. In that year, from 31 Aug. to 11 Nov., azimuths were taken each Monday, Wednesday, and Friday between 1030 and 1330 h LMT. ANOVAs were run to test the null hypothesis, by species, that weekly overall mean directions remained the same.

When the results of one of the ANOVAs made it desirable to analyse what seemed to be a mixture of two normal distributions, the Newton–Raphson algorithm was used to obtain maximum likelihood estimates of the proportion of records belonging to each of the two normal distributions and of the $\bar{x}$ and SD of both distributions (LITTLE & RUBIN 1987).
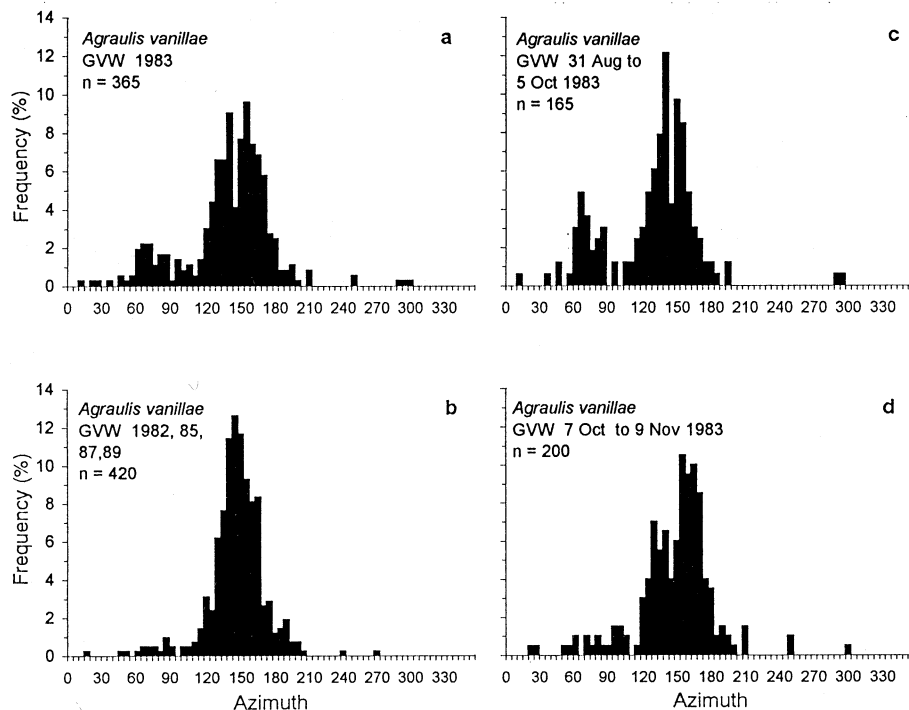
Fig. 3: Histograms of migratory directions from subsets of the *A. vanillae* records from site GVW (Fig. 2 b): (a) 1983, (b) years other than 1983, (c) 1983 prior to 6 Oct., (d) 1983 after 6 Oct

Results. A. vanillae showed significant heterogeneity among weeks (p = 0.038), but *P. sennae* and *U. proteus* did not (p = 0.44 and 0.57). Gross examination of the 1983 records of *A. vanillae* at GVW revealed a bimodality (Fig. 3 a) that was not evident in other sets of records (Fig. 2 a, c–f; Fig. 3 b). In addition to the major mode at $\approx 140°$ there was a lesser mode at $\approx 65°$. Closer examination showed that the lesser mode was much more pronounced early in the season (Fig. 3 c–d), suggesting that the heterogeneity among weeks could be a result of seasonal changes in the relative sizes of the two modes.

Applied to the 1983 *A. vanillae* records, the Newton–Raphson maximum likelihood algorithm estimated that the major mode was at 148° and contained 87 % of the records and that the minor mode was at 64°, with 13 % of the records (Table 4). When 1983 records prior to and subsequent to 6 Oct. were analysed separately, the earlier period had a much larger proportion of minor mode records than the later period (20 vs. 6 %; Table 4 and Fig. 3 c–d). In years other than 1983, minor mode records were only 4 % of the total.

The hypothesis that the seasonal changes in the minor mode were responsible for the significant heterogeneity among weeks for *A. vanillae* azimuths in 1983 was tested by eliminating records with azimuths of 0 to 89°. The ANOVA on this data set revealed no heterogeneity among weeks (p = 0.12).

Table 4:   Analysis of bimodal directions of *Agraulis vanillae* at site GVW, assuming that the bimodality
             stems from a mixture of two normal distributions (Newton–Raphson algorithm)

Time period	% Minor mode	Major mode $\bar{x}$	Major mode SD	Minor mode $\bar{x}$	Minor mode SD
1983	12.7	147.8	27.6	64.3	18.0
1983 before 6 Oct.	20.5	142.4	27.4	64.6	15.2
1983 after 6 Oct.	6.0	151.5	27.2	62.6	24.3
All years	8.4	148.0	23.1	66.1	19.1
All years but 1983	4.2	147.8	19.4	71.1	22.4

Table 5:   Overall mean directions, by year, of *Phoebis sennae* at site GVW. Means followed by the
             same letter are not significantly different (ANOVA, least-square means; p = 0.05)

Year	Inclusive dates	Visits	Number of records	$\bar{x} \pm SE$
1982	3–15 Oct.	3	130	147.1 ± 3.7[b]
1983	31 Aug – 9 Nov.	20	295	136.6 ± 3.1[a]
1985	29 Sept.	1	13	151.6 ± 20.5[ab]
1987	24–29 Sept.	3	241	150.3 ± 2.4[b]
1989	18 Sept.–17 Oct.	7	372	147.1 ± 2.2[b]

Discussion. The anomalous ENE migratory mode of *A. vanillae* at GVW had
no parallel in other species or at GVE (Fig. 2). *P. sennae* at GVW (Fig. 2 a) had
the hint of a minor mode 180 ° from the major one, but the Newton–Raphson
algorithm did not confirm it.

The ENE flights of *A. vanillae* are not easily explained. The fact that such
flights are concentrated in the early part of the migratory season suggests that the
same individuals, or their progeny, may subsequently migrate south-eastward.
Whatever the cause or function (if any) of the ENE flights, they would not have
been detected except for the intensive observations at GVW in 1983. The most
anomalous visit mean for Gainesville (Fig. 1, GVW, *A. vanillae*, 72 °) is for a visit
during which only minor mode directions were recorded for *A. vanillae* (30 Sep.
1983, n = 11).

Year Effects

Azimuths were recorded at GVW during 5 yr in the autumn (1982, 1983,
1985, 1987, 1989), making it possible to test for the occurrence of significant
differences among years in mean migratory directions.

Methods. ANOVA, by species, tested the null hypothesis that mean migratory
directions at GVW did not differ among years. The analysis for *P. sennae* was
repeated using only visits with 15 or more records.

Results. No heterogeneity was revealed among years for *A. vanillae* or *U.
proteus* (p = 0.49 and 0.39). For *P. sennae*, years were heterogeneous (p = 0.027),

with significant differences in OMDs between 1983 and the years 1982, 1987 and 1989 (Table 5).

Discussion. No long-term trends were expected in mean migratory directions and none was detected. For *P. sennae*, the only species with significant heterogeneity, the first and last years of observations yielded the same mean directions. Indeed the one anomaly was that 1983 produced a mean for *P. sennae* 10 ° lower than any other year. Only in 1983 were observations made routinely – good weather or bad, many migrants or few. In other years, observations were made on days selected as likely to yield large numbers of records. To test the hypothesis that this difference in how observation days were selected was a factor in the aberrant mean for 1983, the ANOVA was repeated omitting all visits with fewer than 15 *P. sennae* records. This reduced the number of dates in 1983 from 20 to 4 and dropped the number of records to 185. However, it did not change the results. Year effect was still significant (p = 0.024), and the OMD in 1983 was still significantly more eastward than in 1982, 1987 and 1989. Indeed the OMD of *P. sennae* for 1983 dropped from 137 to 135 °.

In most studies of butterfly migration, directions are not carefully quantified, making year-to-year comparisons difficult. The greatest year-to-year differences are in migrants leaving outbreak areas with no predictable favoured destination, e.g. the emigrations of *Kricogonia lyside* and *Libytheana bachmanii* reported by GILBERT (1985). OLIVEIRA (1990), who quantified dry-season migrations of *Phoebis statira* in Brazil for 2 yr by means similar to those in this study, found no significant differences in mean flight directions between the years.

Site Effects (Gainesville)

A previous study (WALKER 1985) showed that migratory directions at some sites far from Gainesville were different from those measured at GVW. Pilot studies in 1987 suggested that migratory directions at GVE, only 18 km from GVW, might also be different.

Methods. On 2 d in 1987 and 4 d in 1989, azimuths were recorded simultaneously at GVW and GVE. ANOVAs, by species, blocked by date, tested the null hypothesis that OMDs were the same at the two sites. Watson–Williams tests were used to evaluate differences between sites for each species on each date.

Results. Overall mean directions were not significantly different between sites for any of the three species (p = 0.63, 0.10, 0.26 for *P. sennae, A. vanillae, U. proteus*). In 5 of the 18 Watson–Williams tests, the mean directions on a date were different (2 for *P. sennae*, 1 for *A. vanillae* and 2 for *U. proteus*). When probabilities were combined across tests for a species, each species showed significant between-site differences in migratory directions (p < 0.001, 0.025 < p < 0.05 and p < 0.001).

Discussion. Although no differences in overall migratory directions between the two sites were demonstrated, day-to-day variations in mean directions were shown to be discordant – i.e. there was a significant date × site interaction. For example, the mean direction for *U. proteus* on 29 Sep. 1987 was the eastmost of
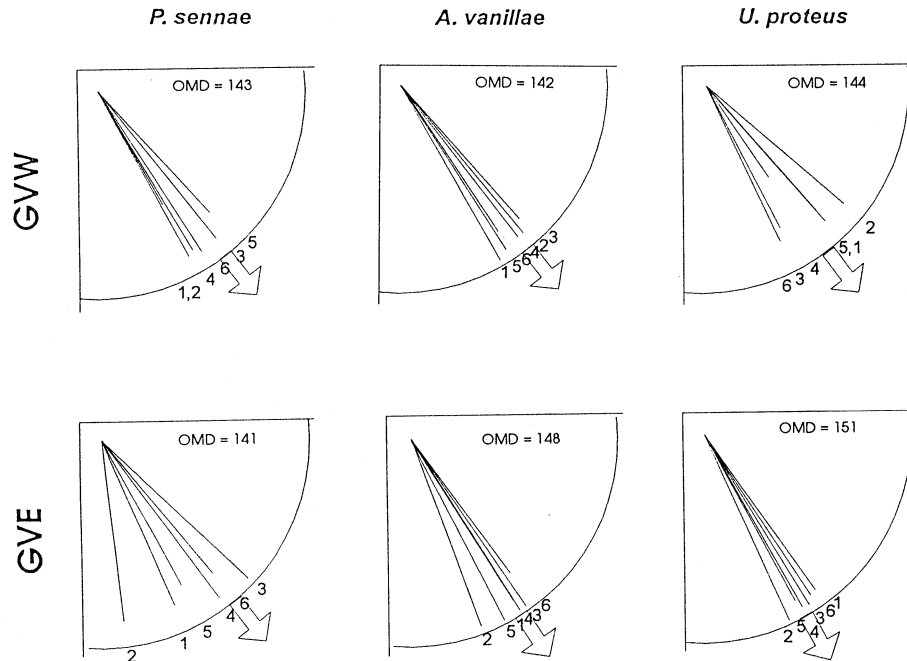
Fig. 4: Mean directions and lengths of mean vectors (r) for the six dates when azimuths were taken simultaneously at GVW and GVE. Numbers on perimeter of arc identify date of observation: 1–2 = 25 and 29 Sep. 1987; 3–6 = 2, 3, 5 and 17 Oct 1989. Other conventions as in Fig. 1

the six at GVW and the southmost of the six at GVE (Fig. 4, visit 2). Whatever causes day-to-day variations does not synchronize the variations at the two sites.

In the geographically extensive part of this study, simultaneous visits to different sites were not feasible, and data could not be blocked by date in the ANOVAs. Without blocking by date in the present ANOVAs, the differences in OMDs at GVW and GVE for *A. vanillae* and *U. proteus* would have been classed as significant (Table 1).

Azimuths Elsewhere in South-eastern United States

The geographically extensive part of this study initially involved a grid of sites in the presumptive source areas of the migrants that pass through Gainesville each autumn. When it became apparent that scarcity of migrants and date-to-date variability in directions made it impractical to establish reliable mean directions at many distant sites, observations were concentrated on two transects positioned to reveal whether mean flight directions of migrants coincide with the most direct overland routes to peninsular Florida (Fig. 5).

Grid

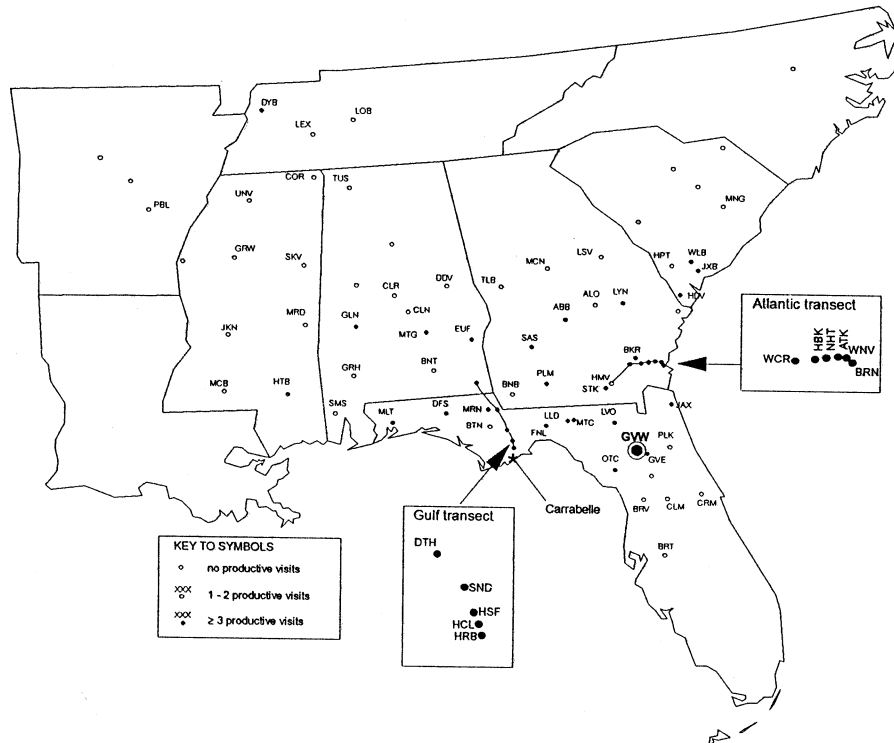*Methods.* Sites were established and observations made during field trips

Fig. 5: Sites visited to observe azimuths of migrating butterflies. Key to symbols at lower left (the ×××in the key to symbols refers to any site code). The three categories of symbols indicate how many visits at that site were 'productive' – i.e. resulted in five or more records for at least one of the migratory species

lasting several days and timed to catch migrations at or near their peaks. All sites were inland, because migrants at the coast do not venture over open sea but generally fly along the coast in one or both directions (NIELSEN 1961; URQUHART & URQUHART 1976). When migrants were plentiful, visits lasted 1 h; when migrants were scarce, observations were ended at ≈2 h unless no other site could be reached that day. Generally only three sites could be monitored in a day. ANOVAs were run by species to test the null hypothesis that overall mean directions were the same at all sites that had three or more 'productive' visits – i.e. visits that yielded five or more records for the species. Records for *P. sennae* with winds >1 ms were deleted before visits were classified.

Results. Records from grid sites totalled 5701. For 11 of the 65 sites, no visit was productive for any species. For 30 sites, one or two visits were productive, and for 24, three or more were (Fig. 5). For *P. sennae* 19 grid sites yielded three or more productive visits and at five of these sites its overall mean direction differed significantly from its OMD at GVW (Table 1, Fig. 6). For both *A. vanillae* and *U. proteus*, six sites yielded three or more productive visits. At one
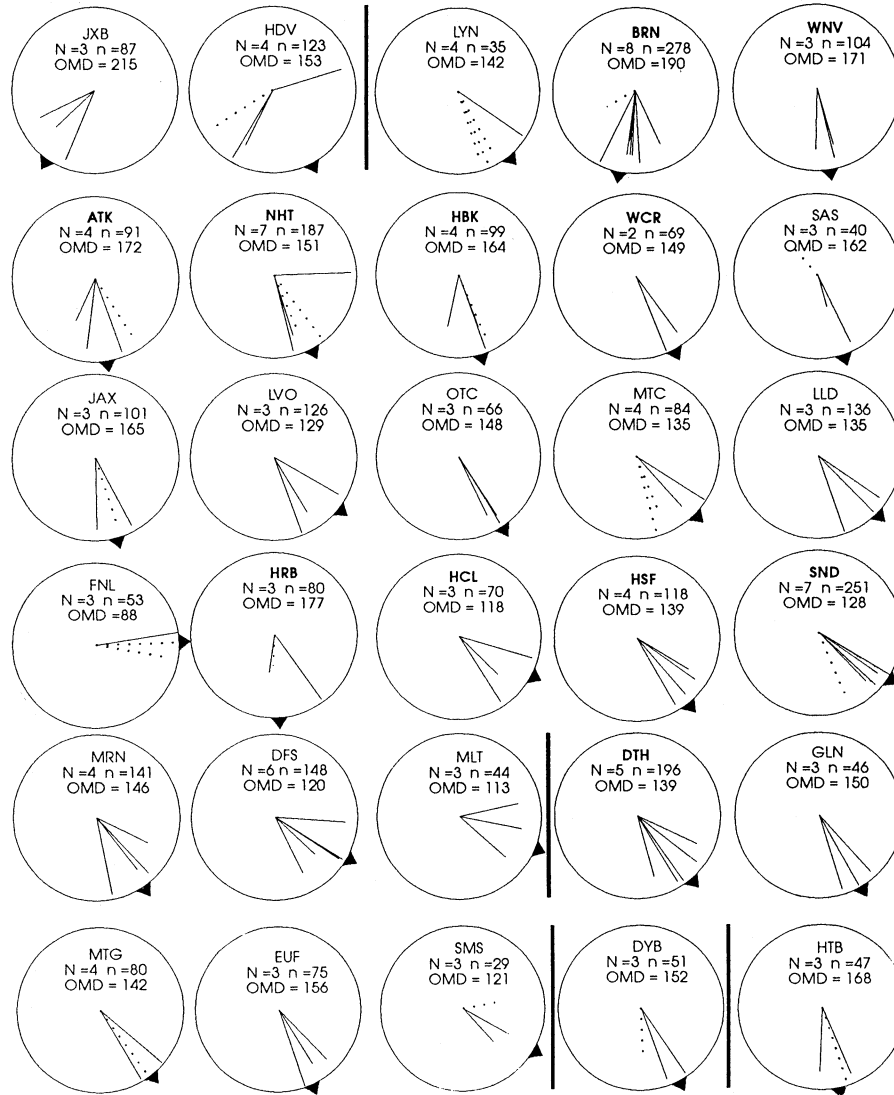
Fig. 6: Mean direction and length of mean vector (r) for all dates when five or more directions for *Phoebis sennae* were recorded at grid sites with ≥3 productive visits and at transect sites. Dotted vectors indicate <10 directions for the date; codes for transect sites are in bold face; vertical bars mark transition to another state; other conventions as in Fig. 1. Sites in South Carolina are in row 1; in Georgia, rows 1–2; Florida, rows 3–5; Alabama, rows 5–6; Tennessee and Mississippi, row 6

of these, JAX in each case, overall mean directions differed significantly from those at GVW (Table 1, Figs 7, 8).

Discussion. In all cases that a species' OMD at a grid site differed significantly from its direction at GVW (n = 7), the deviant direction was more southward or
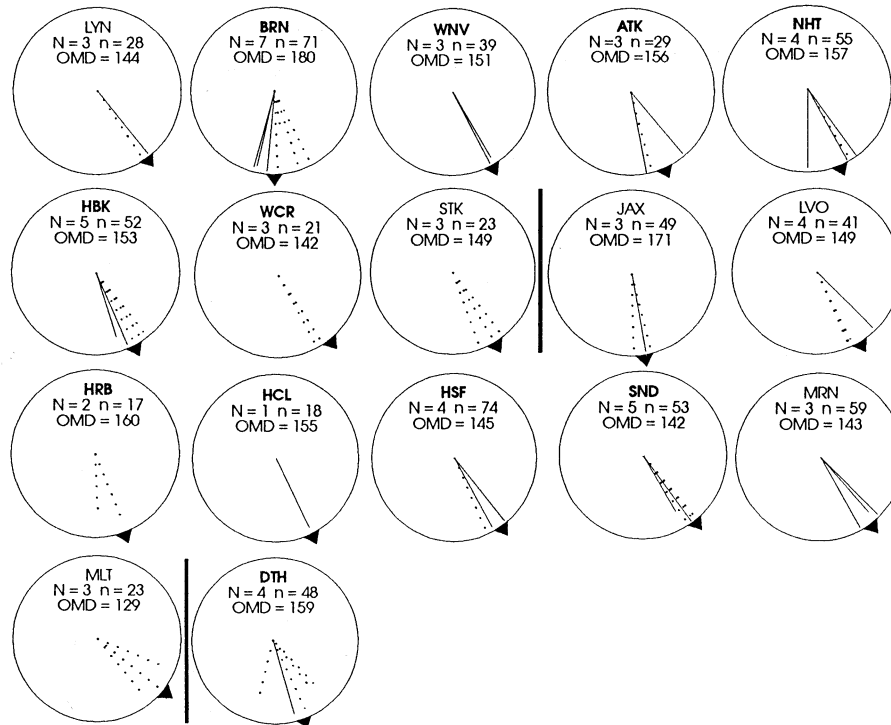
Fig. 7: Mean direction and length of mean vector (r) for all dates when five or more directions for *Agraulis vanillae* were recorded at grid sites with ≥3 productive visits and at transect sites. Conventions as in Figs 1 and 6. Georgia sites, rows 1–2; Florida, rows 2–4; Alabama, row 4

south-westward for sites east of GVW and more eastward for sites west of GVW (Table 1). In the other 24 cases, grid sites manifested directions that were not significantly different from those at GVW, even though OMDs for these sites were often numerically quite different from those for GVW. A major problem with the grid sites was that visit-to-visit variation in mean directions was so great that many visits would be needed to estimate reliably the OMD for a species (Figs 6–8). A related problem was that migrants were often rare or absent at sites inland from the coastal plain. It was initially thought that migration would peak much earlier to the north than at Gainesville, but that did not prove to be the case. Instead, large flights during the migratory season were simply much less frequent.

Gulf and Atlantic Transects

The Gulf coast transect started 5 km inland from Carrabelle, Florida, where the coast runs approximately WSW and ENE. Butterflies that reached this coastline flying S or SE would have to change directions or continue over the Gulf. To get to peninsular Florida by land, they should fly ENE. The Atlantic coast transect started near Brunswick, Georgia, where the coast runs nearly due N and S.
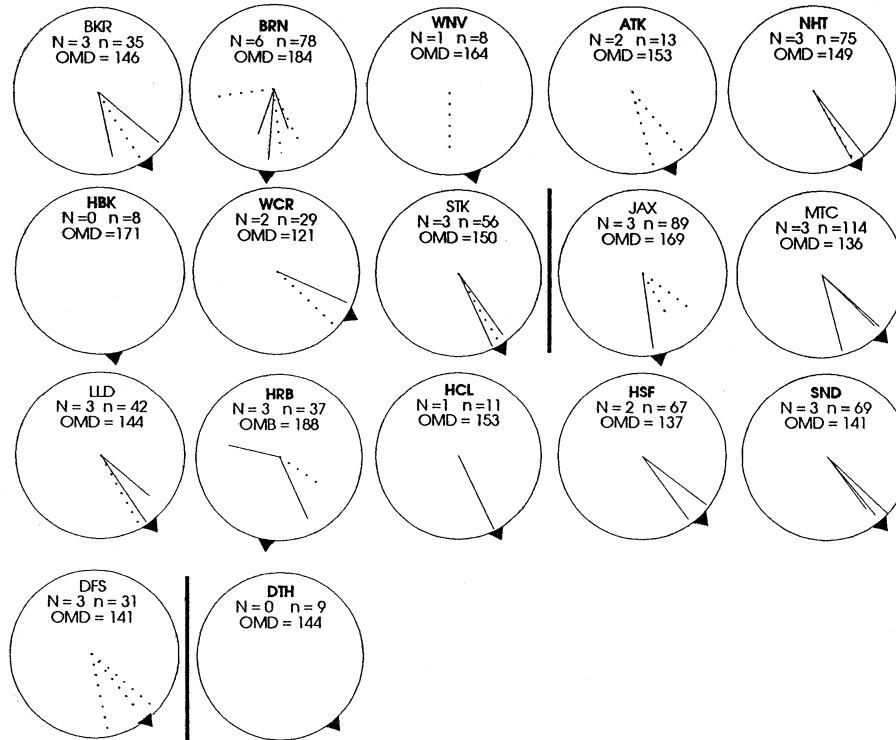
Fig. 8: Mean direction and length of mean vector (r) for all dates when five or more directions for *Urbanus proteus* were recorded at grid sites with ≥3 productive visits and at transect sites. Conventions as in Figs 1 and 6. Georgia sites, rows 1–2; Florida, rows 2–4; Alabama, row 4

Butterflies that reached this coastline flying SE should fly S to avoid flying over the Atlantic and to continue toward Florida.

Methods. Five sites were established along the Gulf transect at distances of 5 to 164 km from the coast, measured inland north-north-westward from the beach at Carrabelle (Table 6). Observations were also made at a field within 100 m of the beach at Carrabelle. Six sites were established along the Atlantic transect at distances of 21 to 93 km, measured inland westward from the beach on Jekyll Island (Table 6). Transect sites were visited an average of 5.3 times and no site received fewer than three visits; however, on some visits one or more of the three species were scarce or absent.

For each transect ANOVAs were run, by species, to test the null hypothesis that overall mean migratory directions along the transect were the same. Transect sites were also included in the ANOVAs of grid sites (Table 1). The Newton–Raphson algorithm was used to estimate parameters for the patently bimodal distribution of *U. proteus* azimuths at Carrabelle.

Results. Records from transect sites totalled 2089. Along the Gulf transect, flight directions for *P. sennae* were heterogeneous (p = 0.040), with the HRB

Table 6: Overall mean directions of migrants at sites along Gulf and Atlantic transects. Directions for the same species and transect that have the same letter are not significantly different (ANOVA, least-square means; p = 0.05)

Site (near)	Km from coast	Overall x̄ migratory direction (±SE)		
		P. sennae	*A. vanillae*	*U. proteus*
Gulf transect				
HRB (Harbeston)	5	177 ± 17[a]	160 ± 12[a]	188 ± 18[a1]
HCL (Hitchcock Lake)	30	118 ± 9[b1]	155 ± 7[a]	153 ± 21[a]
HSF (Hosford)	62	139 ± 6[ab]	145 ± 3[a]	137 ± 9[a]
SND (Sneads)	101	128 ± 5[b1]	142 ± 4[a]	141 ± 10[a]
DTH (Dothan)	164	139 ± 5[ab]	159 ± 5[a1]	144 ± 22[a]
Atlantic transect				
BRN (Brunswick)	21	190 ± 7[a1]	180 ± 5[a1]	184 ± 10[a1]
WNV (Waynesville)	38	171 ± 11[ab1]	151 ± 7[b]	164 ± 25[abc]
ATK (Atkinson)	46	172 ± 11[ab]	156 ± 8[b]	153 ± 13[ab]
NHT (Nahunta)	57	151 ± 7[b]	157 ± 6[b1]	149 ± 6[b]
HBK (Hoboken)	73	164 ± 11[b1]	153 ± 6[b]	171 ± 23[ab]
WCR (Waycross)	93	149 ± 11[b]	142 ± 11[b]	121 ± 9[c1]

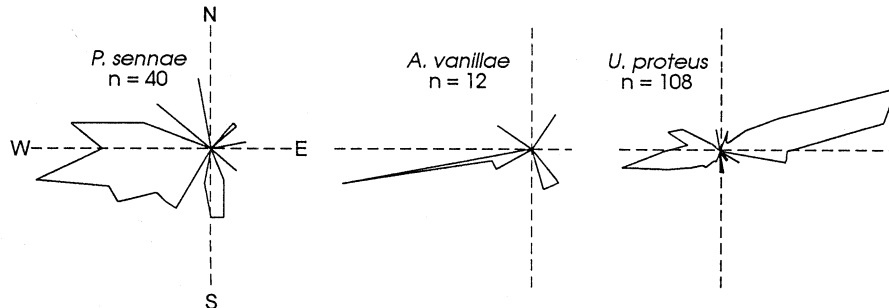[1] Significantly different from overall mean direction at GVW (p ≤ 0.05)

Fig. 9: Polar plots of migratory directions of *P. sennae, A. vanillae* and *U. proteus*, just inland from the ENE – WSW coast at Carrabelle, Florida

site showing a significantly more southward mean than HCL and SND. Flight directions of *A. vanillae* and *U. proteus* were not heterogeneous (p = 0.07 and 0.20). At HLC and SND for *P. sennae*, at DTH for *A. vanillae* and at HRB for *U. proteus*, mean directions were significantly different from GVW. At the field in Carrabelle, few migrants were seen other than *U. proteus*, whose directions were clustered about the two coastwise directions (Fig. 9). The Newton–Raphson algorithm estimated that the two mean directions of *U. proteus* were 71 ° and 251 ° (exactly 180 ° apart!) and that 55 % belonged to the 71 ° mode. The records for *P. sennae* and *A. vanillae* showed single modes that appeared to correspond to the 251 ° mode of *U. proteus*.

Along the Atlantic transect, migratory directions were heterogeneous for all species (p = 0.009 (*P. sennae*), 0.010 (*A. vanillae*), 0.004 (*U. proteus*)), with the BRN site mean significantly more southward than those of many of the more inland sites. For 7 of 18 site–species combinations, the overall mean direction was significantly different from that at GVW (Table 6, Figs 6–8).

Discussion. The Gulf transect failed to show that migrants near the coast were flying appropriately to reach the Florida peninsula by land. At HRB, 5 km from the coast, directions were highly variable with a mean that would predict a concentration of migrants at the coast. Except for *U. proteus*, no such concentration occurred. Indeed the total records for three visits to Carrabelle, HRB, and HCL, each successively farther from the coast, were 40, 53 and 70 respectively for *P. sennae* and 12, 17 and 18 for *A. vanillae*, compared with 108, 37 and 11 for *U. proteus*. A similar avoidance of coastal concentration, especially for *P. sennae*, has been noted for the Atlantic coast – e.g. at Crescent Beach (LENCZEWSKI 1992) and Fernandino Beach (WALKER & WHITESELL, unpubl.). North of the Carrabelle coast's geographic trap for southeast-flying migrants, directions were mostly similar to those at GVW. Two of the four that were significantly different were more eastward, HCL and SND for *P. sennae*, and two were more southward, DTH for *A. vanillae* and HRB for *U. proteus*. The latter site should perhaps be discounted because it is only 5 km from the coast where about half the *U. proteus* flew one coastwise direction (WSW) and the other half flew the other (ENE). WSW led toward a distant dead end of open water at Cape San Blas, while ENE was the most direct overland route to peninsular Florida.

Directions along the Atlantic transect tended to fit the pattern of more southward near the coast and more south-eastward inland. However, this effect was almost entirely due to the overall mean directions at BRN, the site nearest the coast, being 180° to 190° for the three species. Most of the sites along the Atlantic transect were visited fewer than six times and many of the visits produced few records, especially for *A. vanillae* and *U. proteus*. A clearer picture of the changes in mean directions and the variability in these changes awaits a more extensive study of this or a similar transect.

General Discussion

Do Migrants Navigate Toward the Florida Peninsula?

When a pilot study refuted the hypothesis that migrants flew south-eastward to the coast and then followed the coast to Florida, the hypothesis was formulated that migrants somehow knew inland routes to peninsular Florida and followed them. This study suggests that inland movement is usually toward Florida but refutes the existence of well-defined, direct routes that nearly all migrants follow. What becomes of migrants flying south-eastward in the Florida Panhandle is especially puzzling.

One clear message from this study is that mean directions of fall migrants measured at a site vary from date to date (Figs 1, 6, 7, 8). With the exception of *A. vanillae* at GVW in 1983 (Fig. 3 a), there is no persuasive evidence that this

variation is about more than one mode except close to a coast, where migrants sometimes fly coastwise in both directions. However, the data for *P. sennae* from HDV (Hardeeville, SC) are suggestive of two modes: 46 records on 2 Sep. 1990 yielded a mean direction of 73 ° and an r of 0.86, in contrast to 3 other visits with MDs of 207–238 ° (Fig. 6). At two other sites, *P. sennae* had aberrant eastward MDs, and both were also early in the migratory season: NHT (Nahunta, GA), 31 Aug. 1989, n = 20, MD = 88 °, r = 0.94; and PLM (Pelham, GA), 1 Sep. 1990, n = 17, MD = 103 °, r = 0.92, Another example of unexplained variation among visits to a site is the more eastward MDs for *P. sennae* at GVW in 1983 (Table 5).

Although fall migrants in the South-east were discordant in their mean directions, all visits to inland sites with substantial numbers of migrants easily met the Rayleigh test for bias in direction and that direction was never W, NW, N, or NE (except for *U. proteus* flying westward during one visit to HRB, 5 km from an ENE Gulf coast). One dimly revealed pattern is of note: *P. sennae* at inland sites <100 km north of the Gulf often produced OMDs east of SE – that is, SMS (121 °), MLT (113 °), DFS (120 °), SND (128 °), HCL (118 °), FNL (88 °) and LVO (129 °), but not MRN (146 °), HSF (139 °), LLD (135 °) or MTC (135 °). The same species at inland sites <100 km west of the Atlantic often had OMDs S of SSE – JXB (215 °), HDV (if one ignores the eastward mode), BRN (190 °), WNV (171 °), ATK (172 °) but not NHT (151 °), HBK (164 °), WCR (149 °) or JAX (165 °). Neither *A. vanillae* nor *U. proteus* showed a noteworthy eastward bias north of the Gulf. *A. vanillae* showed a slight southward bias near the Atlantic.

An important difference among the three species of this study is that two of them, *A. vanillae* and *U. proteus*, normally overwinter only south of Gainesville. Any individual that fails to get to central peninsular Florida, or to leave offspring that do so, is not genetically represented in subsequent years. On the other hand, *P. sennae* overwinters at Gainesville and northward at least to Valdosta, Georgia, although extremely cold weather may cause some mortality. Thus the species that can best afford not to find peninsular Florida is apparently the best at doing so. Yet *P. sennae*'s direction is more contingent on crosswinds (Table 2), year (Table 5) and perhaps time of day (Table 3) than the other two species. *U. proteus* has the largest population swings and is the most unpredictable as to its occurrence at a site. One of its hosts is soybeans (*Glycine max*), and the historically recent expansion of soybean cultivation may have produced high populations in areas that were virtually unoccupied before – i.e. its summer expansion may be largely contingent on soybean cultivation and its extensive but poorly directed fall migrations may be a recent phenomenon.

To summarize: *P. sennae* shows some ability to navigate toward peninsular Florida, *U. proteus* does not, and *A. vanillae* shows none north of the Gulf but may show some near the Atlantic.

How Do These Migrants Differ from Other Insect and Butterfly Migrants?

There is no doubt that the butterflies in this study actively control their migratory tracks. They fly near the ground where wind speeds are generally less

than their airspeeds, and, when winds become high, they cease to migrate. The
rare times that some individuals can be seen migrating much higher than a few m
above ground or canopy level are always when winds are light or becalmed. *D.
plexippus*, on the other hand, behaves like a skilled glider pilot, circling to gain
altitude in thermals and taking advantage of upper winds when they are in a
favourable direction (GIBO 1986). Other insect migrants, including most moths
that migrate great distances, depend on upper winds for transport but reach them
by direct flight. Only recently has it been shown that such transport is not merely
a matter of which way the winds blow. The migrants evidently read the weather
and take flight at times when the upper winds are in the desired direction of
transport (e.g. TAYLOR & RELING 1986; SMELSER et al. 1991).

Many insects migrate prior to maturation of gametes and some, including *D.
plexippus* in autumn, are in reproductive diapause. The species in this study are
reproductively active during autumn migration and females often are mated and
have mature eggs (WALKER 1978). Direct flights between known feeding and
oviposition sites could account for some of the directions that are not toward
overwintering sites.

Several features of these migrants make them particularly attractive for study.
Their low-altitude flight in daylight and their large size make their migrations easy
to observe directly. Unlike many insect migrants, their numbers are roughly the
same from year to year, with high and low years seldom differing by as much as
an order of magnitude (WALKER 1991 and unpubl.) Finally their theatre of
migration is traversed by good roads and dotted with schools, including major
universities, which should facilitate further studies and cooperative efforts.

Why Don't Migrants Concentrate on Coasts?

One of the most puzzling aspects of the fall migrations of the three species
in this study is that extrapolation of their migratory directions at sites well inland
predicts that large numbers of migrants should reach the coasts, yet coastal
concentrations were modest or lacking. If one assumes that migrants somehow
detect the coast from 20–100 km away and turn aside, the concentration would
be displaced inland and be diluted by being spread over a larger area. Sea breezes,
which are surface winds that blow from ocean to land during the day, offer a
possible means for migrants to remotely sense the coast (MUNN 1966). Sea breezes
occur when the land is warm relative to the ocean, and the cooler, denser ocean
air flows inland beneath the warmer, lighter land air. How far inland a sea breeze
penetrates depends on, among other things, how great is the difference between
ocean and land temperatures. In the fall, the ocean is still warm from summer's
heat and the land no longer gets so hot during the day. Consequently, fall sea
breezes are likely to be weak or lacking and may not penetrate as far as 20 km
inland.

Whether or not sea breezes are involved, there is evidence that fall migrants
form broad rivers rather than maintaining a uniform sheet flow. LENCZEWSKI
(1992) monitored numbers of migrants crossing a Gulf-to-Atlantic transect at the

latitude of Gainesville and found some segments of the transect to be much busier than others.

Another explanation of the lack of expected coastal concentrations of migrants is that individual migrants, near the coast or otherwise, do not fly far. If individuals migrate only a few days before reaching a place to reproduce and die, the coastal areas would be receiving individuals from only a few hundred km inland (5.5 h migration at 5 ms would take an individual about 100 km). A problem with this scenario is that individuals in the northern portions of the summer breeding areas would have to start migrating southward sooner than they apparently do if they were to reach Florida by a succession of generations a few hundred km apart.

What is the Nature of the Migrants' Compass(es)?

Butterfly migrants obviously have some means of maintaining a compass direction independent of the terrain over which they are flying. The nature of their compass(es) is unknown, but a time-compensated sun compass seems likely because many insects in diverse groups have such a compass and because BAKER (1978, 1984) demonstrated a non-time-compensated sun compass in *Pieris rapae*. Further evidence is that the species in this study ceased to migrate when the sky became heavily overcast, although some individuals continued their straight-line flights when a human observer could no longer detect the position of the sun behind the clouds. Opposing the sun being the only compass of butterfly migrants are SCHMIDT-KOENIG's (1985) and GIBO's (1986) observations of monarchs migrating under completely overcast skies and LARSEN's (1993) observations of butterfly migrations in the tropics continuing when the sun is directly overhead.

Another candidate compass is one that detects the Earth's magnetic field. The occurrence of magnetic material in *Danaus plexippus* supports this hypothesis (JONES & MACFADDEN 1982). SCHMIDT-KOENIG (1985) has proposed that this species is able to navigate to México by maintaining a constant angle to magnetic lines of force as proposed for birds by KIEPENHEUER (1984). JUNGREIS (1987) confirmed the presence of biomagnetism in *D. plexippus* but failed to find any in *P. sennae* or *A. vanillae*, two of the species studied here.

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