BUTTERFLY MIGRATION IN THE BOUNDARY LAYER

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ABSTRACT

Long-distance aerial migration by insects is usually at altitudes where wind speeds exceed air speeds of the migrants, restricting their possible tracks to the direction of the wind ± 90°. However, migrating butterflies generally fly near the ground where wind speeds are low enough to permit progress in any direction. Three species of such boundary-layer migrants are conspicuous in southeastern United States each fall: ***Phoebis sennae*** (cloudless sulphur), ***Agraulis vanillae*** (gulf fritillary) and ***Urbanus proteus*** (long-tailed skipper). Migrants fly in a straight line within a few meters of the surface. At a given locality their tracks usually cluster about a single direction. Based on observations at Gainesville, Florida, mean direction changes little with time of day, season, or direction of wind. Mean direction changes significantly with geographical locality in a pattern which suggests navigation by the butterflies and a destination of peninsular Florida. For example, in northern Alabama and Mississippi the mean direction of ***P. sennae*** is ca. 135°, whereas in south-central Georgia it is ca. 155°, and near the Atlantic coast in south Georgia and north Florida it is ca. 175°. Migrants moving down the Florida peninsula each fall may number 11−16 million ***A. vanillae***, 29−48 million ***P. sennae*** and 41−396 million ***U. proteus***.

INTRODUCTION

Most migrating insects fly at altitudes where wind speed exceeds their air speed (Johnson 1969). Consequently, their direction of movement must fall within the semicircle toward which the wind is blowing. Radar studies generally show that high altitude migrants are flying with the wind—i.e., their heading approximates the direction of the wind, and their velocity approximates the sum of their air speed and the wind speed (Pedgley 1982).

On the other hand some insects migrate in their ***boundary layer***, the layer of air near the ground where wind velocity is less than the insects' air speed. The thickness of the boundary layer for a particular migrant depends not only on the profile of wind speed vs. height but also upon what air speed the migrant can maintain (Taylor 1958, Pedgley 1982). Insects in their boundary layer can progress in any direction and are generally close enough to the surface to make feasible their study by direct observation.

Butterflies are the best known boundary-layer migrants among insects (Williams 1930, 1958; Baker 1978). Most species can be identified in flight, and individuals can be followed visually far enough to yield a reliable measurement of the migrant's track. In southeastern United States at least eight species of butterflies migrate southward each fall (Walker 1978, 1980; Urquhart and Urquhart 1978). This paper deals with the three that are especially abundant and easy to recognize in flight: ***Phoebis sennae*** (cloudless sulphur), ***Agraulis vanillae*** (gulf fritillary) and ***Urbanus proteus*** (long-tailed skipper).

GENERAL ASPECTS OF MIGRATION

During winter each of the three species is restricted, in eastern United States, to a small portion of its summer range. ***A. vanillae*** and ***U. proteus*** overwinter only in peninsular Florida and ***P. sennae*** only in the Gulf region. During summer they move northward, regularly breeding at least as far north as Kansas and Virginia (Walker 1978). The movement northward each spring is seldom discernible, but provided the contrast between summer and winter ranges is correct, it must occur. The movement southward each fall is often conspicuous and can be regarded as a flight toward suitable overwintering grounds.

Observable fall flight paths of ***P. sennae***, ***A. vanillae*** and ***U. proteus*** are remarkably straight. Typically, from the time the butterfly comes into view until it disappears, its track changes no more than a few degrees. When the migrant encounters an obstacle such as a building or a dense wood, it flies up and over rather than deviating to either side. Over open ground, migrants seldom fly higher than 2 m (Fig 1).

The low height of flight and the behavior of migrants when they encounter a barrier make it feasible to construct flight traps that catch migrants and that keep separate those migrants that encountered the trap from one direction (± 90°) and those that encountered it from the opposite direction (± 90°) (Walker 1978, 1980). I have operated such traps at Gainesville during seven falls and seven springs. The traps are oriented perpendicularly to the axis of the Florida peninsula in order to distinguish migrants flying down the peninsula from those flying toward Georgia. For ***P. sennae***, ***A. vanillae*** and ***U. proteus*** the traps have documented large-scale fall flights southward; for ***P. sennae*** and ***A. vanillae*** they have revealed small-scale spring flights northward (Table 1).

The numbers of migrants fluctuate substantially from one fall to the next. Documentation of this annual variation comes from operating the same 6-m long, 3-m high hardware-cloth flight trap at the same site for five years (1979–83) (see Fig 5B in Walker 1980). The numbers of fall migrants were lower in 1983 than for any previous year (Fig 2). This pattern correlates with record droughts in the northwestern portion of the summer breeding area.

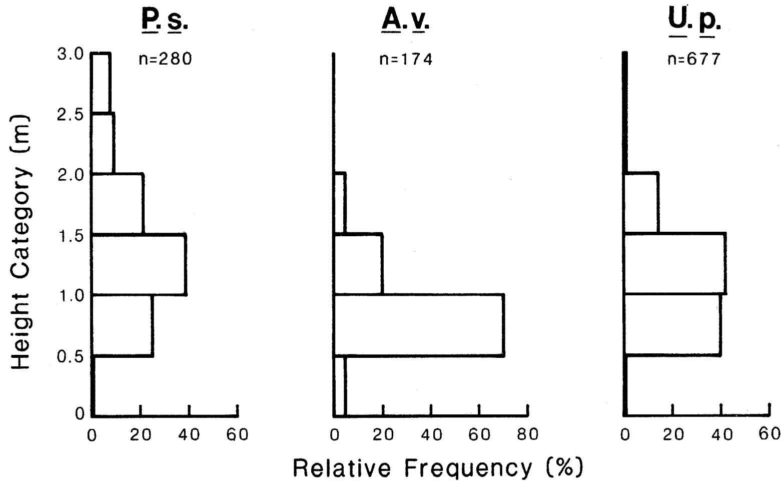

Figure 1

Frequency distribution of heights of three species of butterflies migrating across an open field, Gainesville, Florida, 31 Aug–12 Oct 1983. Uppermost category includes all individuals flying above 2.5 m. ***P.s.* = *Phoebe sennae*, *A.v.* = *Agraulis vanillae*, *U.p.* = *Urbanus proteus***. (Heights were recorded as migrants flew between 3-m tall poles which were marked at 1-m intervals; 15-min observation periods began at 1130 and at 1230 h LMT, 3 days per week.)

The timing of fall flights through Gainesville were similar each year, and differences among the three species were minor (Fig 3). The flights start in early September and conclude in early November. Approximately 50% of the fall migration occurs between mid-September and mid-October (see also, Walker and Riordan 1981).

Nearly 50% of fall migrants at Gainesville are males, and 20–80% of the females have already mated at least once (Walker 1978). Mean air speed of migrants has been measured at 4.8 ***(A. vanillae)*** to 6.1 $m \cdot s^{-1}$ ***(U. proteus)*** (Arbogast 1966, Balciunas and Knopf 1977).

DIRECTIONS OF FALL MIGRANTS: EXPERIMENTAL PLAN

Butterflies that breed in areas as widely separated as Kansas and Virginia must find their way to common winter ranges or perish. For example, ***A. vanillae*** and ***U. proteus*** in eastern United States survive winters only in south Florida. The study here reported was designed to monitor directions of fall flights throughout the summer breeding ranges to learn whether migrants have a common destination, and if so, what routes are taken to it.

Widespread monitoring of flights on a modest budget requires that observations at an average site be limited to one or a few dates, times of day and weather conditions. Yet it is important to know whether these variables affect the directions taken by fall migrants. Consequently I divided my efforts into two components: (1) brief observations of directions at many localities which collectively represented as much of the summer breeding ranges as I could reach and (2) intensive study of directions at Gainesville, where observations could be made at all times of season and

Table 1
Direction of flights as revealed by catches in flight traps perpendicular to the axis of the Florida peninsula, Gainesville, Florida, 1975–1983.

Species	Fall			Spring		
	North-flying	South-flying	% S	North-flying	South-flying	% N
Phoebis sennae	165	2186*	93	19**	1	95
Agraulis vanillae	28	757*	96	16**	2	89
Urbanus proteus	92	3562*	97	1	1	50

* Directions of fall flights biased southward ($p_\alpha < 0.005$).

** Directions of spring flights biased northward ($p_\alpha < 0.005$).

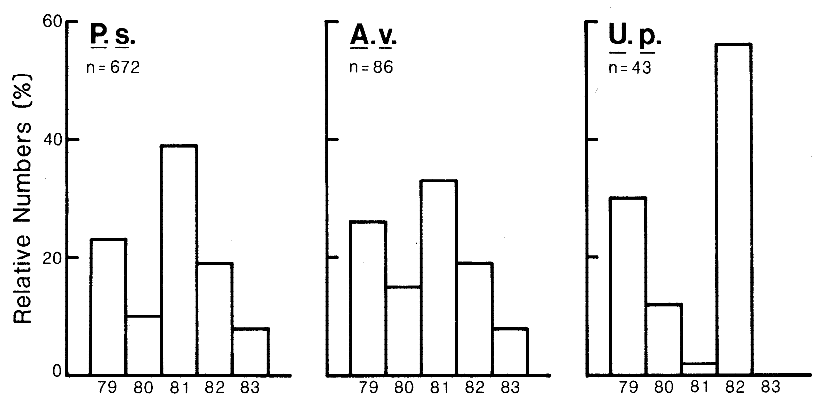

Figure 2
Annual changes in numbers of three species of fall migrants, Gainesville, Florida, 1979–1983, based on catches of one permanent flight trap; data are expressed as percent of 5-year catch. (Total catch of *U. proteus* is low because trap efficiency for that species is close to nil; indeed none were caught in 1983.)

day and under a full spectrum of weather conditions. The hope was that by thoroughly understanding fall directions at one site, scant records from other sites could be correctly interpreted.

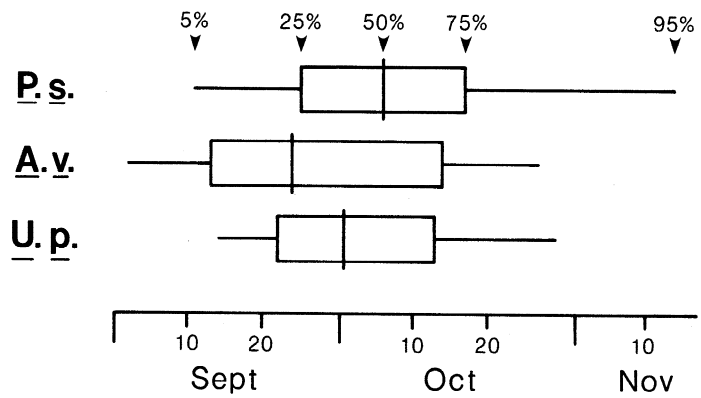

Figure 3
Average progression of fall migration as revealed by flight-trap catches, Gainesville, Florida, 1978–83. Vertical line is date that median migrant was caught; horizontal bar is middle 50% of migration; horizontal line is middle 90%. Differences between species were not consistent from year to year except that ***A. vanillae*** migration reached 5 and 25% completion earliest and ***P. sennae*** reached 95% latest. (Total samples: ***P. sennae*** = 748, ***A. vanillae*** = 244, ***U. proteus*** = 1057.)

DIRECTIONS AT GAINESVILLE

Methods

All observations of flight directions at Gainesville were made in the central portion of a 8-ha bahiagrass field at University of Florida's Green Acres Farm (29°41′N, 82°30′W). Preliminary observations were made Oct 1982. In 1983, two assistants alternated in measuring migratory directions each Monday, Wednesday, and Friday, 31 Aug to 11 Nov 1030–1330 h LMT (local mean solar time, based on local longitude). (At Gainesville, LMT = EDT (eastern daylight time, based on 15° time zone) −90 min). The procedure for determining a migratory direction was to spot a straight-flying butterfly, walk or run to where it had just been, and with a sighting compass (SUUNTO KB-14) read the magnetic bearing of its direction of disappearance. In addition to magnetic bearing (later converted to true bearing) the following data were noted for each record of migratory direction: time (standard time, later converted to LMT), species, blue sky visible (% of total), appearance of sun (disc bright, hazy, obscured or partly obscured), wind direction (as indicated by a 0.3-m plastic ribbon dangling from the ring end of a horizontal laboratory thermometer attached at 1 m to a slender post), wind speed (as measured by a Dwyer pith-ball anemometer) and air temperature at 1 m (the thermometer bulb was shaded by a plastic shield, 3-cm dia. × 10 cm).

As soon as a record was entered on the data sheet, visual search for another migrant began. At times of peak migration as many as 80 records were taken in an hour. Bias in selecting butterflies for observation was minimized by scanning perpendicular to the approximate axis of migration and selecting the first straight-flying butterfly whose path could be reached.

On six days, migration directions were measured during the entire period of migration (ca. 0800–1700 h LMT). Migratory directions were grouped by species, time of season, date, and time of day, and the following statistics calculated: mean direction (M.D.), length of mean vector (*r*), 95% confidence interval of M.D. (Batschelet 1981).

Results

Time of Season — Mean migratory directions remained approximately the same throughout the season and were similar for the three species (Figs 4,5). The principal difference among species was that during the first two-thirds of fall migration the distribution of ***A. vanillae*** directions was bimodal, whereas ***P. sennae*** and ***U. proteus*** each manifested a single mode of migratory direction throughout the fall. Their single modes approximated 141°, as did the greater of the two ***A. vanillae*** modes (Fig 4). The minor ***A. vanillae*** mode (ca. 63°) was not evident after 14 October.

During the first few weeks of migration, directions of ***P. sennae*** were more variable than during the remainder of the season, as shown by the ***r*** values and (for given sample sizes) confidence intervals (Figs 4, 5). (No confidence intervals were calculated for ***A. vanillae*** mean directions during the first 7 weeks because the assumption of a circular normal distribution was violated.)

Time of Day — All records of directions summarized in Figures 4 and 5 were taken during 1030–1330 LMT. Whether mean direction changed with time of day was addressed by pooling observations at hourly intervals for the six days of daylong observation (Fig 6). No temporal trends are evident in ***U. proteus*** or ***A. vanillae***. ***P. sennae*** was more variable, but only one hourly M.D. was significantly different from 141°.

Crosswinds — When butterflies encounter crosswinds, they can sometimes be seen to turn their headings toward the wind—a behavior that reduces or negates drift (Williams 1958). The effects of crosswinds on fall migratory direction of ***P. sennae*** and ***U. proteus*** at Gainesville were judged by comparing directions on days with right and left crosswinds. Only two days (5 Oct, 4 Nov) had large numbers of migrants and consistently left (NE) crosswinds (Fig 7). ***P. sennae*** did not fully compensate, but ***U. proteus*** apparently did. (***A. vanillae*** was not analyzed because numbers were low and the distribution of migratory directions was sometimes bimodal.)

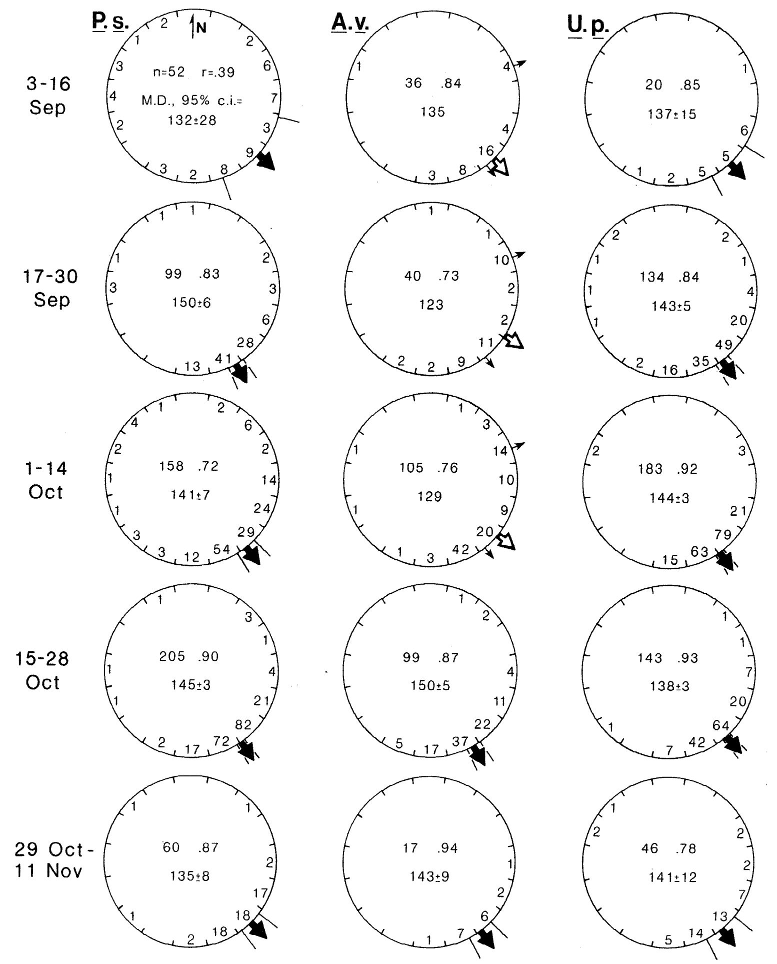

Figure 4

Directions of fall migrants, biweekly periods, Gainesville, Florida 1983 (1030–1330 h LMT). Within each circle are frequency distributions of true bearings (grouped at 22.5° intervals), number of observations, length of mean vector (*r*), mean direction (M.D.) and, where frequency distribution is appropriate, 95% confidence interval of M.D. Outside each circle is an arrow indicating mean direction and, where appropriate, lines defining the 95% confidence interval. For first three biweekly periods of ***A. vanillae***, small arrows indicate estimated directions of the two modes (viz. 63° and 141°).

Discussion

With some noteworthy exceptions, mean directions of fall migrants at Gainesville remained close to 141° regardless of species, time of season, time of day, or wind. If I had recorded migratory directions at Gainesville for only a few hours on one or a few dates, the mean migratory directions of any of the three species would likely have been ca. 141° but could have deviated from that value by 10 or more degrees.

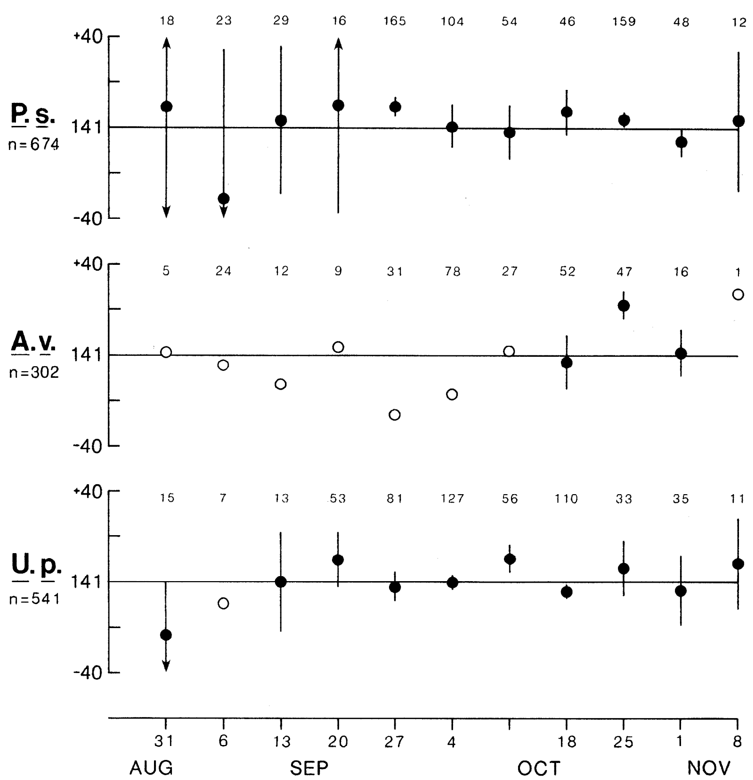

Figure 5

Direction of fall migrants, weekly periods, Gainesville, Florida, 1983 (1030−1330 h LMT). Each dot shows mean direction relative to 141°. Sample size is above each dot. For solid dots, vertical line shows 95% confidence interval (arrows indicate that c.i. exceeds the limits of the graph). Open dots indicate that distribution of directions was bimodal or that ***n*** was too small to determine a confidence interval.

The early season bimodality of *A. vanillae* directions at the Gainesville site is unexplained. No minor mode was evident in records made during pilot studies in 1982 nor at other localities in 1983. Minor mode directions were especially prevalent during midday, a time that corresponds to a decline in migratory activity (Fig 8).

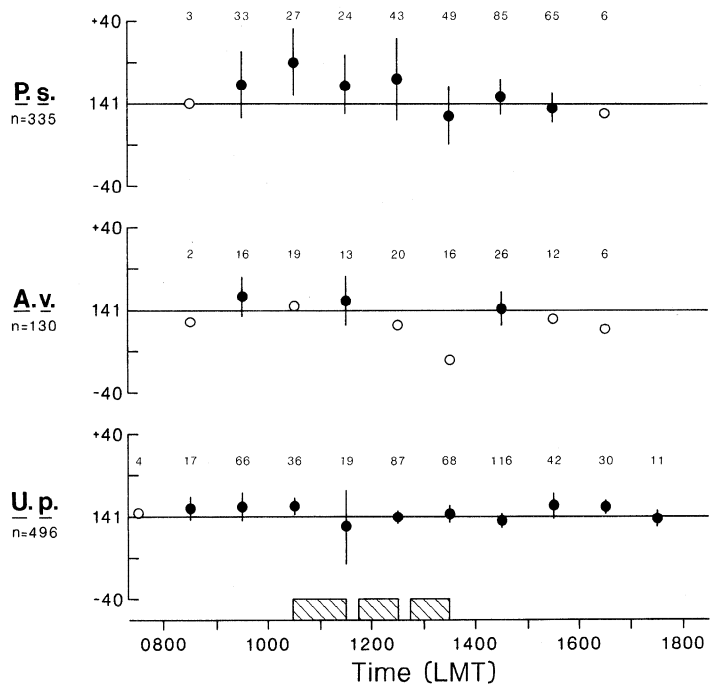

Figure 6

Direction of fall migrants, hourly periods, Gainesville, Florida; 3, 11, 15 Oct 1982; 3, 4, 7 Oct 1983. Same conventions as Figure 5. Hatched areas at bottom show times of observation for Figures 4, 5, 7.

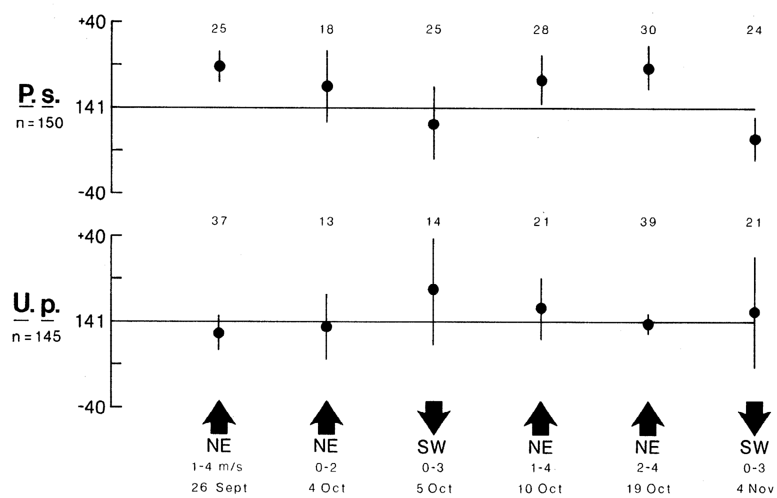

Figure 7

Mean directions and 95% confidence intervals of ***P. sennae*** and ***U. proteus*** in left (NE) and right (SW) crosswinds, Gainesville, Florida, 1983 (1030–1330 h LMT). Arrows above wind information show direction of effect of wind if migrants do not fully compensate.

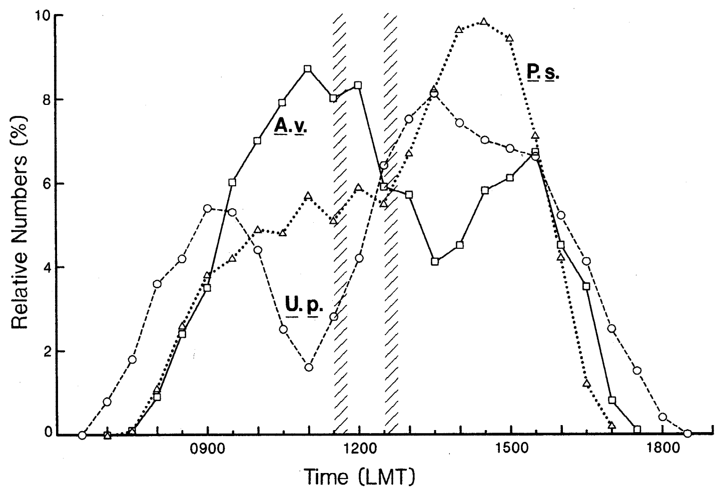

Figure 8

Half-hourly trends in numbers of migrants, based on counts during 4 days (11, 15 Oct 1982; 3, 4 Oct 1983) at Gainesville, Florida Hatched bars show 15-min periods during which routine counts of migrants were made during fall 1983 (see Table 2). Moving three-point average was used to smooth data for each day and the values plotted here are the averages of the normalized data for each of the four dates.

DIRECTIONS ELSEWHERE

Literature Records

P. sennae are brilliant yellow and therefore conspicuous in their migratory flights. This has contributed to there being a significant number of published reports of directions of their fall flights (Fig 9). A remarkable feature of these reports is that they agree that the flight direction is "southeast" (no further quantification) when the locality is inland and that the direction is coastwise when the locality is near the coast. A map of the records (Fig 9) suggests this hypothesis: ***P. sennae*** (and perhaps ***A. vanillae*** and ***U. proteus)*** from all over southeastern United States arrive at suitable overwintering grounds by flying southeast until they reach a coastline. They then follow the coast (with an eastward or southward component if they are to reach peninsular Florida). Specimens that head northward along the north Atlantic coast are probably doomed—and especially likely to be reported (e.g., Muller 1977, Pyle 1981).

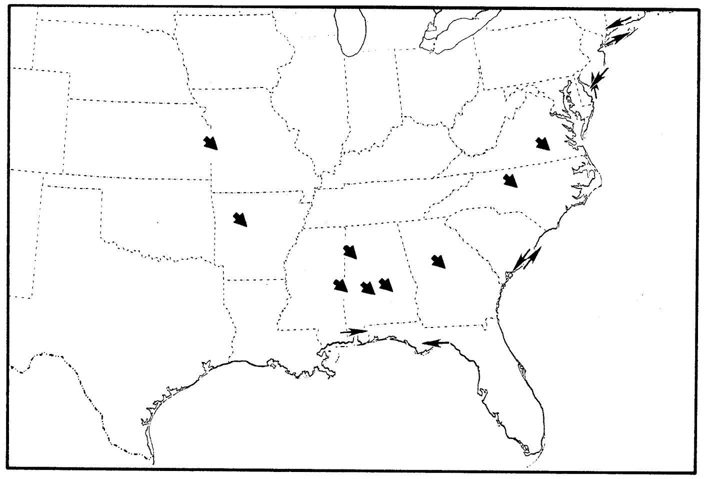

Figure 9

Literature records of direction of fall migration of ***Phoebis sennae*** (Shannon 1916; Williams 1930, 1958; Clark and Clark 1951; Lambremont 1968; Howe 1975; Urquhart and Urquhart 1976; Muller 1977; Gaddy and Laurie 1983). Inland, the direction has always been southeast; coastal records have been parallel to the coast.

Methods

During fall 1982 and 1983, 30 localities in southeastern United States were visited one to four times to observe directions of migrating butterflies (Fig 10). Localities were generally established at intervals of ca. 100 km along east-west lines. At each locality an observation site was selected for its openness, extent and accessibility. Playing fields and school campuses were frequent choices. If a site better than the one first chosen was subsequently found, observations were thereafter made at the new site. All sites were at least 10 km from the coast and salt-influenced communities.

Flight directions were generally determined in the same manner as at the Gainesville (GVL) site. However, when migrants were scarce, the number of records was increased by this procedure: if a butterfly was spotted close enough to watch but too far to reach, a line was estimated parallel to the flight path of the migrant and its azimuth was measured. Directions taken in this manner did not differ significantly in mean direction from those taken (at the same site and observation period) by reaching the flight path of the migrant.

Dates, times and conditions of observation and numbers of records by species are given in Appendix 1.

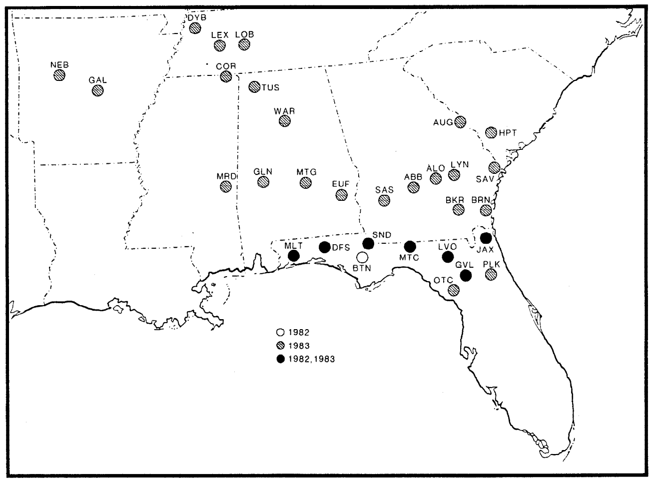

Figure 10
Localities for observing fall migrations, 1982–83.

Results

Results are detailed in Appendix 2 and summarized (for ***A. vanillae*** and ***P. sennae***) in Figure 11.

Only the data for ***P. sennae*** are geographically extensive. Mean flight directions for northern Mississippi (COR), northern Alabama (TUS) and central Alabama (MTG) were 133 ± 3, 136 ± 4 and 138 ± 5, respectively. On the other hand, mean directions in central Georgia (ABB, ALO, LYN) were 154 ± 10, 152 ± 5 and 160 ± 12. Finally, mean directions in southeast Georgia (BRN) and northeast Florida (JAX) were 185 ± 11 and 163 ± 4. With the exception of two west Tennessee localities (DYB, 166 ± 14; LEX, 153 ± 14), mean directions for ***P. sennae*** were essentially toward the Florida peninsula. Data for ***A. vanillae*** (Fig 11) and ***U. proteus*** (Appendix 2) are similar to the ***P. sennae*** data but are restricted to localities in north Florida and south Georgia.

Discussion

The hypothesis that all inland fall flights are in the same direction is refuted and an alternative hypothesis is supported—viz. that inland flights are principally toward peninsular Florida.

Earlier records for ***P. sennae*** migrations agree with the new hypothesis as well as with the old, except records in North Carolina (Shannon 1916, p. 228; arrow on map, no numbers) and Virginia (Clark and Clark 1951, p. 114; "many individuals of this species all flying toward the southeast across the road").

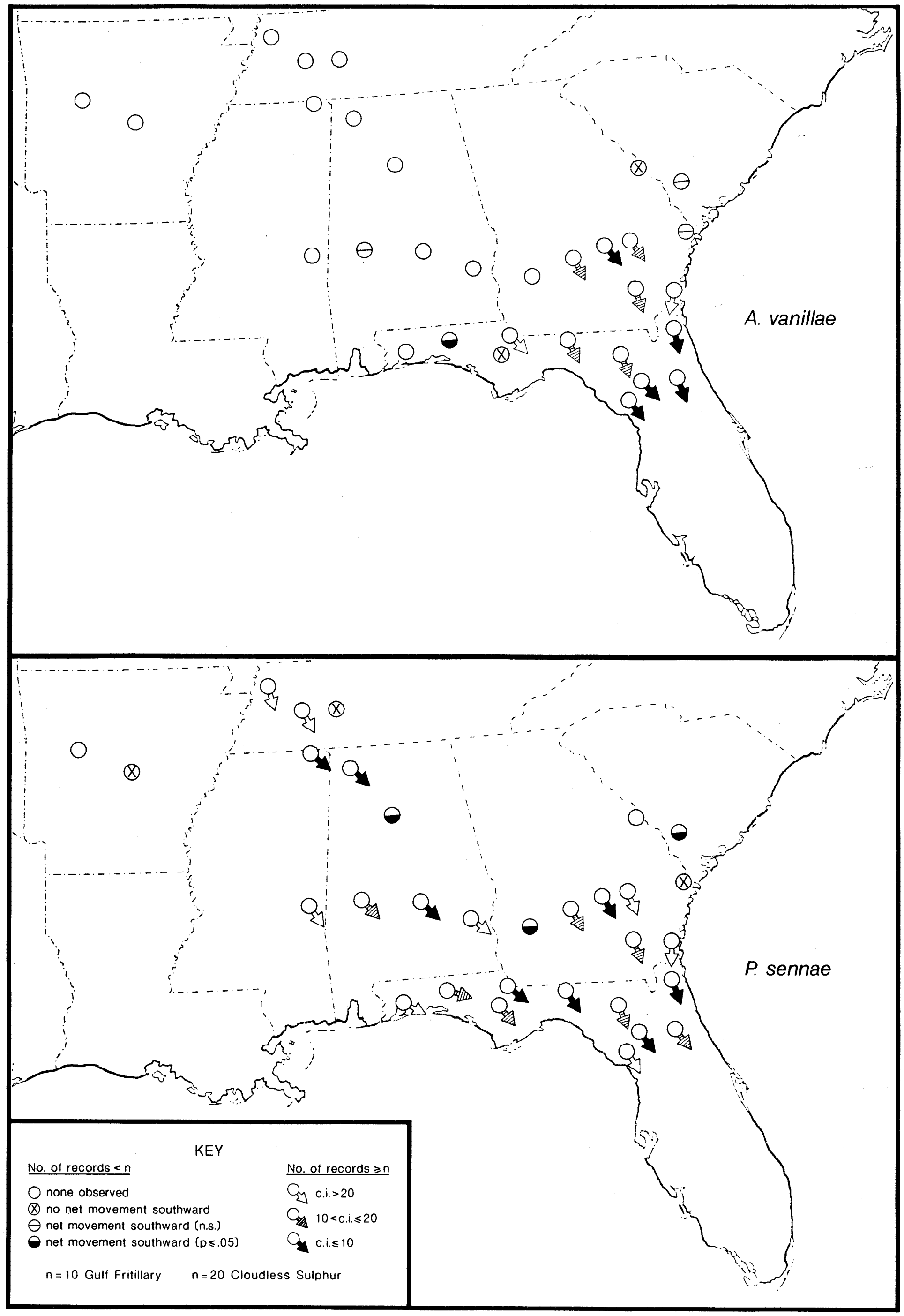

Figure 11
Summary of mean directions of *A. vanillae* and *P. sennae* during fall migration, 1982–83. (See Appendix 2 for detailed data.)

Monarch butterflies *(Danaus plexippus)* in eastern North America have the same sort of task as ***P. sennae***, ***A. vanillae*** and ***U. proteus***—i.e., to reach a common overwintering area from widely separated summer breeding areas. Their migratory flights differ from the ones described here in destination (central Mexico) and character (soaring flight at high altitude is common: Gibo and Pallett 1979, Gibo 1981, Brower, Schmidt-Koenig, this volume). Schmidt-Koenig (1979, this volume) studied directions of ***D. plexippus*** in their fall flights and reported significantly different directions at Ithaca, New York, and Blue Ridge, North Carolina. The directions, 224° and 215°, do not point toward a common destination, but Schmidt-Koenig (this volume) noted that they are in close agreement with a magnetoclinic model of pathfindng.

NUMBERS OF MIGRANTS

Methods

Numbers of migrants flying southward through north peninsular Florida were estimated by two independent methods. The first used polyester flight traps (see Walker 1980, Walker and Riordan 1981). The second method, effected in fall 1983, depended on counting migrants as they flew between 3-m PVC poles at the GVL site. Every Monday, Wednesday and Friday, 31 Aug to 11 Nov, at 1130 and 1230 LMT, 15-min counts were made of ***P. sennae*** and ***A. vanillae*** that flew over a 45-m ENE-WSW line and of ***U. proteus*** that crossed the first 15-m of the line. Each 15-min count consisted of three 5-min periods separated by 1-min intervals. Butterflies that flew northward over the line were subtracted from those that flew southward.

Converting 15-min counts to estimates of total migration for a day required knowing how relative density of migrants varied as a function of time of day. This was studied by taking 15-min counts every 30 minutes during each of four days (Fig 8). These data indicated that 2.6% (***U. proteus***) to 8.0% (***A. vanillae***) of total migrants for a day flew during the 15-min periods beginning at 1130 and 1230 LMT. Because counts were made 3 of every 7 days during the migratory season, the counts were further adjusted by a factor of 2.33.

Results

Results of the two procedures are compared in Table 2. Estimates for ***P. sennae*** and ***A. vanillae*** are surprisingly consistent. ***U. proteus*** numbers show greater changes, but the values confirm visual impressions: in 1975 ***U. proteus*** seemed exceptionally abundant; in 1978 ***U. proteus*** seemed exceptionally rare.

The estimates in Table 2 are for net movement southward across an ENE-WSW line at Gainesville. For example, in fall 1983, 2,345,000 more ***U. proteus*** were estimated to have flown southward across each km of ENE-WSW line than flew northward. Total migration through north peninsular Florida depends on the ENE-WSW limits of migratory flights and the average density of net movement between

Table 2
Estimates of absolute numbers of fall migrants (1000's per km^2), Gainesville, Florida.

	Phoebis sennae	***Agraulis vanillae***	***Urbanus proteus***
Polyester traps[a]			
"1975"[b]	368	126	3956
1978[c]	480 ± 112	159 ± 75	406 ± 148
15-min counts[d]			
1983	292	113	2345

[a] 2 or 4, 6-meter flight traps; trapping efficiency estimated to be 10%

[b] 18 Sept to 26 Nov 1975, 26 Aug to 17 Sept 1976; 2 traps

[c] 29 Aug to 12 Nov 1978; 4 traps (mean estimate and 95% c.i.)

[d] Migrants counted 6 times weekly (MWF, at 1130 and 1230 h LMT) as they flew over a 45-m (*P. sennae, A. vanillae*) or 15-m (*U. proteus*) line, 31 Aug to 11 Nov 1983. Proportion of daily flight occurring during two 15-min counts estimated to be 0.050 for *P. sennae*, 0.080 for *A. vanillae* and 0.026 for *U. proteus* (Fig 8).

these limits. Fall migration occurs at least from Otter Creek to Palatka (Fig 10: OTC, PLK) an ENE-WSW distance of ca. 106 km. The only estimates of migration density are at GVL. Taking the ENE-WSW limits to be 100 km and the average density of net movement to be the same as at GVL, one can estimate total net movement of butterflies southward during a fall, in millions, by moving the decimals in Table 2 one place to the left—e.g., 234 million *U. proteus* in 1983. Other estimates range from 11 million *A. vanillae* in 1983 to 396 million *U. proteus* in 1975.

Discussion

The similarity of estimates made by independent methods suggests that estimates of migration density at GVL are correct within a power of 10. Estimates of total migration through north peninsular Florida, made by extrapolating the GVL results approximately 50 km toward both the Gulf and the Atlantic, are likely to be more inaccurate. To improve estimates of total fall migration, estimates of migratory density (absolute or relative to GVL) should be made at intervals across north peninsular Florida.

UNANSWERED QUESTIONS

While these studies clarified certain features of the fall migrations of ***P. sennae***, ***A. vanillae*** and ***U. proteus***, they highlighted four unanswered questions.

How do migrants orient?

That ***P. sennae***, ***A. vanillae*** and ***U. proteus*** can maintain a compass direction is evident. How they do it is not. The two most orthodox possibilities are that they employ a time-compensated sun compass or a magnetic compass. The fact that fall migrants maintain their migratory direction on overcast days (though few fly) weakens but does not eliminate the sun compass hypothesis (Verheijen 1978). The fact that neither ***P. sennae*** nor ***A. vanillae*** have detectable biomagnetism weakens but does not eliminate the magnetic compass hypothesis (Jungreis 1982, Schmidt-Koenig, personal communication).

Do migrants navigate?

Figure 11 suggests that migrant ***P. sennae*** have a map as well as a compass—i.e., that they navigate as well as orient. Alternatives to a navigational hypothesis are (1) the pattern of ***P. sennae*** migratory directions is fortuitous, (2) the pattern reflects migrants orienting by the sun with the eastward component of their movements causing their clocks to lag behind sun time, sending them more southward, and (3) migrants are genetically programmed to fly along particular axes (thus the descendents of those that fly NW in the spring fly SE in the fall, etc.). The lagging-clock hypothesis assumes that migrants use time-compensated sun orientation (unproved) and that most south Georgia and north peninsular Florida migrants have recently come from the northwest. The genetic-program hypothesis becomes hard to defend if migrants from diverse sources interbreed in south Florida during the winter (unknown).

The geographical area most important for testing the navigational hypothesis is eastern Virginia and North Carolina. Here migrants should fly SW prior to turning S and SSE into Florida. An attempt to measure directions in that region in late Sept 1983 was canceled upon finding no migrants at Augusta, Georgia, and very few at Hampton, South Carolina (Fig 10; AUG, HPT). The literature records from inland in this area are anecdotal but do not support the navigational hypothesis (Fig 9; Shannon 1916; Clark and Clark 1951).

What is the origin of GVL migrants?

This question emphasizes that no direct evidence exists as to how far individual ***P. sennae***, ***A. vanillae*** or ***U. proteus*** fly. Circumstantial evidence suggests that some individuals which fly through Gainesville have come from as far away as Kansas or Missouri. If a migrant maintained a speed of 5 $m \cdot sec^{-1}$ for 5 hours each day, it could fly from Columbia, Missouri, to Gainesville, Florida, in 15 days (1350 km at 90 $km \cdot day^{-1}$). During their fall migration, monarchs fly more than twice that distance (Urquhart and Urquhart 1978).

What is the destination of GVL migrants?

I have made no observations of fall migrations in peninsular Florida south of Gainesville and know of no records for ***P. sennae***, ***A. vanillae*** or ***U. proteus*** except for ***A. vanillae*** and ***U. proteus*** flying southward along the coast at Indialantic (about 175 km down the peninsula from GVL) (Williams 1958, p. 41).

If tens, or hundreds, of millions of migrants pass through north peninsular Florida each fall (Table 2 and text), what becomes of them? These numbers compare favorably with numbers of monarchs at overwintering sites in Mexico (Brower 1977), yet no one has reported spectacular aggregations of butterflies in (well-explored) south Florida. Two facts are worth noting: south Florida is large enough to hold millions of nonaggregated butterflies without their making a spectacle, and ***U. proteus***, the most numerous migrant, is individually inconspicuous. To illustrate the former fact, 400 million ***U. proteus*** distributed evenly over the four southernmost Florida counties (Dade, Monroe, Collier, Broward) would amount to 1 ***U. proteus*** per 408 m^2 (or 13 per American football playing field).

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