

# Butterfly Migrations in Florida: Seasonal Patterns and Long-Term Changes

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**ABSTRACT** Flight traps at Gainesville, in north-central Florida, operating from 1984 to spring 2000, separated butterflies migrating into the Florida peninsula ( $SSE \pm 90^\circ$ ) from those migrating out of the Florida peninsula ( $NNW \pm 90^\circ$ ). Five species flew southward in the fall and northward in the spring: *Phoebis sennae* (L.), *Agraulis vanillae* (L.), *Junonia coenia* (Hübner), *Urbanus proteus* (L.), and *Eurema lisa* (Boisduval & LeConte). Five species had significant northward flights in spring but no significant migration in fall: *Pieris rapae* (L.), *Vanessa virginiensis* (Drury), *Vanessa atalanta* (L.), *Eurytides marcellus* (Cramer), and *Libytheana bachmanii* (Kirtland). *Danaus plexippus* (L.) had a southward flight in fall but no significant migration in spring. *Eurema daira* (Godart) switched from a net movement northward in early fall to a net movement southward in late fall, whereas *Eurema nicippe* (Cramer) maintained a net movement northward throughout the fall. The major migrants differed significantly in the seasonal timing and duration of peak migration. When the numbers trapped were greatest, the proportion of those flying in the migratory direction was greatest. The numbers of spring migrants of *A. vanillae* increased during the course of the study, whereas both the spring and fall migrations of *J. coenia* declined. The fall migrations of *P. sennae* and *U. proteus* declined sharply. In 1990-1999, the fall migrations of *P. sennae* and *U. proteus* averaged only 37 and 15% of what they had averaged in 1984-1989. Reduced planting of soybeans in source areas for migrants probably contributed to these steep declines.

**KEY WORDS** *Phoebis sennae*, *Agraulis vanillae*, *Junonia coenia*, *Urbanus proteus*, *Eurema lisa*, phenology

THE MIGRATORY FLIGHTS of butterflies are more easily studied than those of other insects because butterflies are easily identified on the wing and their migrations usually occur near the ground during daylight (Baker 1984, Walker and Littell 1994, Oliveira et al. 1998). Migrant butterflies, unlike locally flying ones, generally maintain their flight direction from the time they are first seen until they disappear from sight. When they encounter an obstacle, such as dense woods or a building, they rise and fly over it rather than altering their direction. This behavior makes it possible to develop flight traps that continuously monitor butterfly migrations. Beginning in 1975, I have used bi-directional, linear flight traps to study butterfly migrations near Gainesville, FL. The earliest traps were inefficient and difficult to maintain (Walker 1978, 1980), but by 1984 I had permanent traps, made largely of hardware cloth, that intercepted migrants flying within  $\approx 3$  m of the ground. Each trap was 6 m wide and erected perpendicular to the principal directions of migratory flights, which are parallel to the long axis of the Florida peninsula. I previously reported and interpreted trapping results through 1988 (Walker 1991). In this article I extend the observations through the spring of 2000 and use the larger samples and longer time period to refine earlier conclusions and to

revise the conclusion that the numbers of migrants are notably constant.

## Materials and Methods

**Flight Traps.** The primary flight trap in this study was the "model #3," erected on an ENE-WSW line in a pasture near Gainesville, FL ( $82^\circ 27' 19''$  W,  $29^\circ 40' 22''$  N) (Walker 1985b). This trap has a 6-m-wide, 3.7-m-tall, 13-mm mesh hardware-cloth barrier that intercepts butterflies flying within 3.3 m of the ground. Those that attempt to continue their linear track by flying over the barrier enter a duct that leads them through valves into holding cages. Butterflies encountering the trap from the south (actually  $158 \pm 90^\circ$ ) and from the north ( $338 \pm 90^\circ$ ) are led to separate cages, permitting estimation of net movement northward or southward across the 6 m monitored by the trap. The #3 trap was operated every spring and fall from 1984 through spring 1997. Regular operation resumed in spring 1999 and continued through spring 2000. During most of this study a second 6-m flight trap, slightly different from the #3, was operated in line with and immediately to the WSW of the #3 trap. During fall 1985, this trap was the #4 (Walker 1985b). Before spring 1986, it was modified slightly to become the #5 (Walker 1991). The #5 trap was operated in spring during 1986-1991, 1994-1997, and 1999-2000,

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Table 1. Numbers and directions of butterflies trapped during spring and fall migrations near Gainesville, FL, 1984 to 2000

Species	Spring (5 Mar to 3 June)			Fall (27 Aug to 2 Dec)		
	N	S	%N	S	N	%S
<i>Phoebis sennae</i>	624	93	87***	13,994	1,063	93***
<i>Agraulis vanillae</i>	1,346	28	98***	16,003	600	96***
<i>Junonia coenia</i>	5,606	512	92***	2,411	448	84***
<i>Urbanus proteus</i>	23	10	70*	5,466	341	94***
<i>Eurema lisa</i>	93	44	68***	584	251	70***
<i>Pieris rapae</i>	204	57	78***	4	7	36
<i>Vanessa virginiensis</i>	391	177	69***	4	6	40
<i>Vanessa atalanta</i>	40	7	85***	0	1	—
<i>Eurytides marcellus</i>	236	163	59***	17	13	57
<i>Libytheana bachmanii</i>	20	4	83**	0	2	0
<i>Danaus plexippus</i>	0	1	—	12	4	75*
<i>Eurema daira</i>	18	12	60	621	631	50
<i>Eurema nicippe</i>	30	19	61	1,123	1,520	42***

Results of chi-square test of no. northward = no. southward indicated by \*,  $P < 0.05$ ; \*\*,  $P > 0.01$ ; and \*\*\*,  $P < 0.001$ .

and in fall during 1986–1989, 1992–1996, and 1999. To summarize, the #3 trap was operated for 14 falls and 16 springs. In 11 falls and 14 springs a second, similar, trap was operated. In addition, the #3 trap was operated in the fall of 1997 from 1 to 17 October.

Throughout the study the spring migration period was defined as the 13 wk from 5 March to 3 June, and the fall period was defined as the 14 wk from 27 August to 2 December (Walker 1991). Every 7 d during these periods, the traps were emptied two to seven times (usually three times), with the last emptying being the catch of the last day of the 7-d period. Butterflies taken from the traps were either killed or taken elsewhere, to prevent their being counted more than once.

The number of individuals caught flying in the migratory direction would be a species' gross migration. Throughout this article, "migration" refers to net migration, calculated by deducting from the gross migration the number of individuals trapped flying in the nonmigratory direction.

**Seasonal Patterns.** For species with >200 individuals captured, seasonal changes in the proportion of individuals flying in the migratory direction were quantified by calculating what percent of the total catch of the species each week were individuals caught in the side of the trap facing the migratory direction. Seasonal changes in the numbers of migrants were quantified as the weekly number of migrants of a species expressed as a percent of the total number of migrants for a season. For these calculations, capture records were summed by date across years and without regard to trap. Records for fall 1997 were omitted because they were not for a complete migratory season. Data for the spring and fall of 1988 were omitted for most species because those record sheets were lost after I had extracted the data for the first four species in Table 1.

**Numbers of Migrants.** Numbers of migrants caught in the #3 trap were used to estimate long-term changes in the numbers of migrating *Phoebis sennae* (L.), *Agraulis vanillae* (L.), *Junonia coenia* (Hübner), and *Urbanus proteus* (L.). For *Vanessa virginiensis* (Drury), *P. rapae* (L.), and *E. lisa* (Boisduval & Le-

Conte), the numbers trapped were low with a concomitant low correlation between the catches of the two traps. Therefore, the average numbers of migrants for the two traps, rather than the numbers caught in trap #3, were used to estimate the long-term changes in numbers. For the four season-years when only trap #3 was operated, that trap's catch was used as an estimate of what the average would have been had both traps been in operation.

The only data for fall of 1997 were from the #3 trap from 1 to 17 October. These data were used to estimate the numbers the #3 trap would have caught during the entire fall, based on the average proportion of migration in other years occurring during this 17-d period. For the four species so estimated, these proportions were 0.265 (*P. sennae*), 0.295 (*A. vanillae*), 0.437 (*J. coenia*), and 0.234 (*U. proteus*).

The entire data set for this article is accessible at <http://csssrrv.entnem.ufl.edu/~walker/ftdata.htm>.

**Statistics.** Chi-square was used to test the hypotheses that numbers of a species trapped flying northward and southward were equal. For the four species with the greatest numbers of migrants ( $n > 500$  for all years), the dates of 25, 50, and 75% completion of migration were noted for each species, year, and season whenever the migration was 30 or more individuals. For each species and season, Levy's Tukey-type test was used to make multiple comparisons among medians and among the durations of the middle 50% of migration (Zar 1984). Confidence limits for flight trap catches were based on the Poisson distribution (Zar 1984). To detect changes in the relative efficiency of the #3 and its companion trap, I compared their estimates of the larger migrations by correlating, for each species and season, the net numbers of migrants caught by the two traps (Microsoft 1997). To qualify for the analysis, a species had to have a migration totaling >1,500 for the two traps in the season in question. Long-term changes in the levels of migrations were evaluated by regressing log numbers of migrants trapped in the #3 trap against years (Microsoft 1997).

## Results

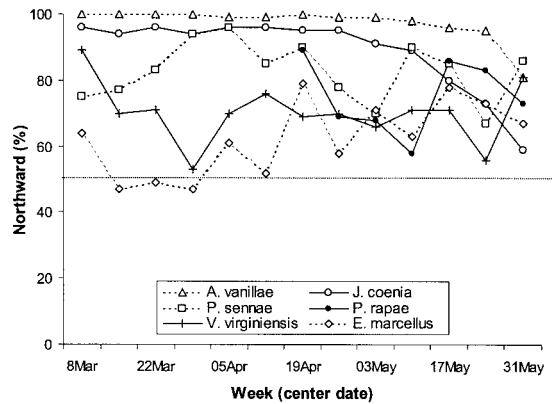
**Migrant Species.** Thirteen species of known or suspected migrants were trapped in sufficient numbers to justify keeping and analyzing records of capture (Table 1). Five of these flew mostly northward in spring and mostly southward in fall: *Phoebis sennae*, *Agraulis vanillae*, *Junonia coenia*, *Urbanus proteus*, and *Eurema lisa*. Five flew mostly northward in spring but demonstrated no significant southward migration in fall: *Pieris rapae*, *Vanessa virginiensis*, *V. atalanta* (L.), *Eurytides marcellus* (Cramer), and *Libytheana bachmanii* (Kirtland). *Danaus plexippus* (L.) showed a significant southward movement in fall with no northward movement in spring. *Eurema daira* (Godart) had nearly equal numbers flying southward and northward in fall. Overall, *Eurema nicippe* (Cramer) showed a significant northward movement in fall. Specifically, in four of 13 falls, significantly more *E. nicippe* were trapped flying one direction than the other ( $P < 0.05$ ); in each case, the net movement was northward. In seven other falls, the net movement was northward, but not significantly so.

**Seasonal Patterns.** Fig. 1A shows at weekly intervals the percent of captured butterflies flying  $337.5 \pm 90^\circ$  (northward) in the spring for the six species with  $n > 200$ . Fig. 1B shows the percent of captured butterflies flying  $157.5 \pm 90^\circ$  (southward) in the fall for the seven species with  $n > 200$ . *E. daira* began the fall with a net movement northward and ended the fall with a net movement southward. During the first 4 wk, 61% (148 of 244,  $P < 0.001$ ) were trapped flying northward; during the last 4 wk, 57% (276 of 484,  $P < 0.01$ ) were trapped flying southward.

Figures 2 and 3 show the changes in the relative net numbers of the principal migrants at weekly intervals during the spring and fall. Table 2 gives the mean dates for completing 25, 50, and 75% of spring and fall migrations for those species in which the migration in a season, summed across years, exceeded 500. *P. sennae* and *J. coenia* were half done with their spring migration significantly earlier than was *A. vanillae*. The middle 50% of the spring migration of *P. sennae* was significantly shorter than that of either *A. vanillae* or *J. coenia*. However, the middle 50% of the fall migration of *P. sennae* was significantly longer than that of *J. coenia* and *U. proteus* but not of *A. vanillae*. The date of median fall migration for *U. proteus* was significantly later than the dates for *P. sennae* and *A. vanillae*.

**Numbers of Migrants.** Fig. 4 shows the annual variation in net migration. Correlation coefficients for net migrations recorded by the #3 trap and the #4 or #5 trap in seasons in which traps were run at both positions were as follows: *P. sennae* (fall), 0.96; *A. vanillae* (fall), 0.98; *J. coenia* (fall), 0.97, (spring), 0.95; *U. proteus* (fall), 0.97 ( $n = 13$  for spring and 11 for fall). Regression analyses showed a significant decline in the numbers of three of the four principal fall migrants: *P. sennae* ( $P < 0.001$ ), *J. coenia* ( $P = 0.028$ ), and *U. proteus* ( $P < 0.001$ ). Among the spring migrants, *J. coenia* showed a significant decline ( $P = 0.001$ ),

## A Spring



## B Fall

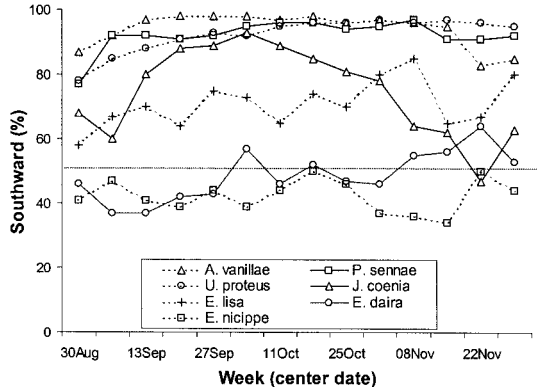


Fig. 1. Seasonal pattern of migrations: weekly percentages of individuals trapped that were flying in the main migratory direction, Gainesville, FL. All species with  $n > 200$  during a season are graphed for that season. The dashed line at 50% separates areas of the graphs that indicate net movement in opposite directions. (A) Percent flying northward in spring, 1984–2000. (B) Percent flying southward in fall, 1984–1999.

whereas *A. vanillae* and *P. sennae* showed significant or near-significant increases ( $P = 0.011$  and  $0.053$ ).

## Discussion

**Migrant Species.** Migrating *P. sennae* and *A. vanillae* are generally numerous enough during the fall in north peninsular Florida that only a few hours of observations will establish a statistically significant net movement in the migratory direction. However, the spring migrations of these two species and the spring and/or fall migrations of other species are too sparse for the migrants to demonstrate their migration quickly. Here the directional traps, operating continuously during entire migratory seasons, demonstrate their power. Most of the migrations in Table 1 had been established previously (Walker 1991); however, the northward spring migrations of *E. lisa*, *V. atalanta*, *E. marcellus*, and *L. bachmanii* had not. These species had originally seemed too scarce or nondirectional in

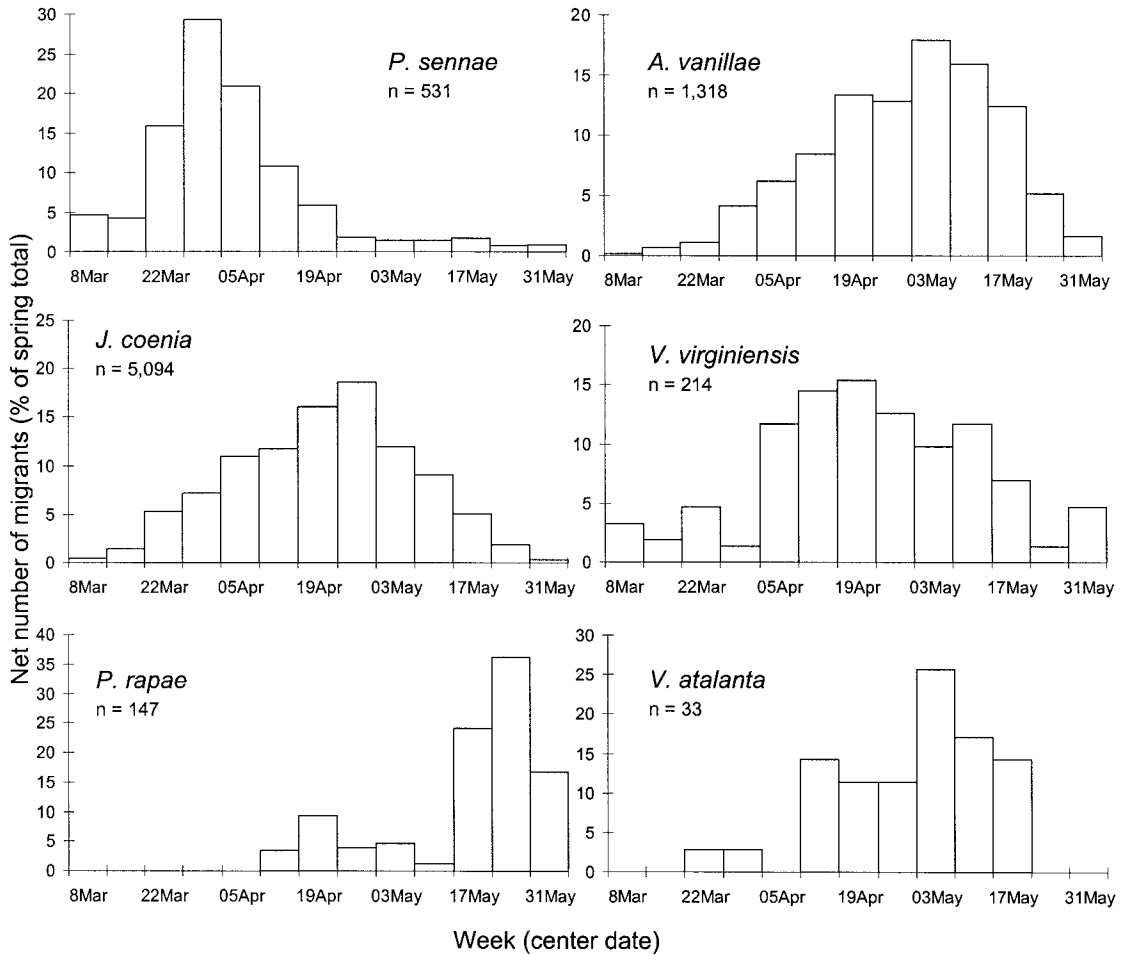


Fig. 2. Seasonal pattern of spring migrations: weekly net numbers of northward migrants as percentage of total net number, Gainesville, FL, 1984–2000.

spring to merit record keeping. The 13-mm mesh of the hardware-cloth barriers of the traps was too coarse to keep some species from passing through. Two species earlier detected as southward fall migrants with traps made of mosquito netting fall into this category: *Lerema accius* (Smith) and *Panoquina ocola* (Edwards) (Walker 1978). *E. दौरा* and *E. lisa* could pass through 13-mm mesh, but, rather than doing so, at least some individuals followed the routes of the other migrants and reached the 6-mm mesh holding cages. *Urbanus dorantes* (Stoll) showed significant southward movement in fall in the earliest flight-trap study (Walker 1978), but in most years of the current study none was captured; and, when some were, no southward bias was evident.

Scott (1986) reports that all the species identified as migrants in this study annually expand their ranges northward in North America beyond their year-round range. In some species the expansion is slight (e.g., *E. marcellus*, *V. atalanta*); in others the temporary range more than doubles the year-round range (e.g., *J. coenia*, *L. bachmanii*). As Williams (1958) and others

have pointed out, migration from a permanent breeding ground to a temporary one presents an evolutionary dilemma unless there are return flights. If the migration is always out and never in, individuals in the permanent breeding area have no ancestors that showed the migratory habit, and individuals that produce migrants contribute less to the next generation than they might otherwise. Nonetheless, five migrants showed significant net movement northward in spring with no indication of a southward movement in fall.

The low numbers of migrant *D. plexippus* were, in part, a result of their often migrating well above the height of flight traps. The species' southward movement in fall in peninsular Florida is in accord with the Knight et al. (1999) conclusion that the permanent monarch population she studied in south Florida received an influx of migrants in the fall. The monarchs that breed in the Gainesville area in March and April come largely or entirely from the Mexican overwintering colonies rather than being the descendants of monarchs that during the previous fall migrated to

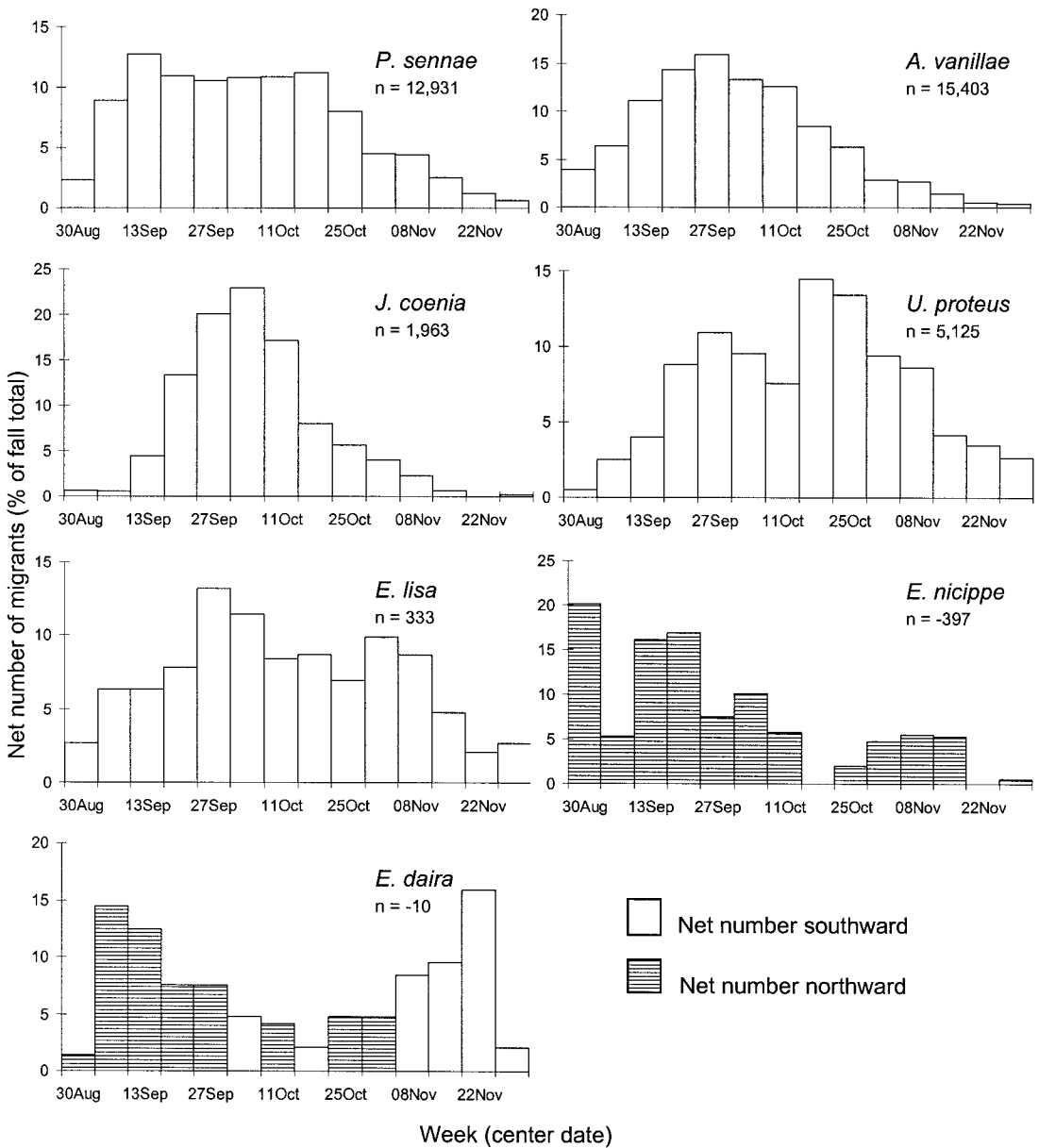


Fig. 3. Seasonal pattern of fall migrations: weekly net numbers of migrants as percentage of total net number, Gainesville, FL, 1984–1999. For *Eurema nicippe* and *E. daira*, *n* is negative because more were trapped flying north than flying south.

south Florida, Cuba, or beyond (Malcolm et al. 1993, Knight et al. 1999).

**Seasonal Patterns.** The species that migrated in greatest numbers generally had a high percentage of individuals flying in the migratory direction throughout the season. During the peak weeks of their migrations, directionality for these species exceeded 90%. In weeks in which their net migrations were relatively low, as at the beginning or end of the season, directionality was often low. For example, for the three most numerous fall migrants (*P. sennae*, *A. vanillae*, and *U. proteus*), the percent of trapped indi-

viduals flying in the migratory direction exceeded 90% for most of the season, and every week of lower directionality was near the beginning or end of the season (Fig. 1B). *P. coenia* was the only species for which the spring sample of migrants exceeded 5,000. Its directionality was >90% for the first 9 of the 13 wk of spring but declined to 59% by the 13th week. *A. vanillae* maintained a remarkable directionality of >95% until the last 2 wk of the spring season (Fig. 1A).

The traps were not quite at right angles to the directions of migration. At a site 4 km west of the trapping site I estimated the mean direction of *P.*



Table 2. Mean dates of completion of 25, 50, and 75% of major spring and fall butterfly migrations and the interquartile range (duration of the middle 50% of migration), Gainesville, FL, 1984 to spring 2000

	No. of years <sup>a</sup>	25%	50% <sup>b</sup>	75%	Interquartile range (days) <sup>b</sup>
Spring migration					
<i>P. sennae</i>	8	25 Mar	30 Mar a	6 Apr	12a
<i>A. vanillae</i>	14	21 Apr	3 May b	11 May	21b
<i>J. coenia</i>	16	10 Apr	19 Apr ac	30 Apr	20b
Fall migration					
<i>P. sennae</i>	14	15 Sep	2 Oct a	18 Oct	33a
<i>A. vanillae</i>	14	16 Sep	30 Sep a	13 Oct	27ab
<i>J. coenia</i>	14	25 Sep	4 Oct ab	13 Oct	18cd
<i>U. proteus</i>	13	30 Sep	15 Oct b	25 Oct	25bd

<sup>a</sup> When the net number of migrants for a species in a season was less than 30, that season for that year was omitted.

<sup>b</sup> Dates or numbers with the same letters (in the same column segment) do not differ significantly (i.e.,  $P_{\alpha}$  exceeds 0.05).

*sennae*, *A. vanillae*, and *U. proteus* in the fall to be 146, 142, and 142° (Walker and Littell 1994), whereas the traps were perpendicular to SSE (157.5°). This discrepancy should have minimal effect because the directions flown by migrants cluster about the mean direction and, to a much lesser extent, about its reverse (Walker 1985a).

The early, compact spring migration of *P. sennae* (Fig. 2; Table 2) probably results from individuals that overwintered in central peninsular Florida flying north in spring before producing a new generation. However, *A. vanillae* and *J. coenia* evidently produce at least one generation south of Gainesville before their spring migrations. In the case of *J. coenia*, such reproduction explains how the numbers of northbound migrants in spring can exceed the numbers of southbound migrants the previous fall (Fig. 4). The significant differences in the seasonal pattern of the fall migrations of the principal migrants (Fig. 3; Table 2) have no evident explanation, but the phenologies of their food plants in source areas would merit investigation in this regard.

**Numbers of Migrants.** Permanent flight traps allow the numbers of migrants to be quantified continuously during migratory seasons year after year. Counts of migrants by visual observation are limited in duration, and fatigue or bias may affect their accuracy. On the basis of the first 5 yr of trapping with the current traps, I concluded that the numbers of the principal migrants were "notably uniform" from year to year compared with most other butterfly migrations reported in the literature (Walker 1991). Now that the records are for 14 or more years, long-term declines and increases are evident in the migrations of the four principal migrants (Fig. 4).

The increase in the number of spring-migrating *A. vanillae* that began in 1989 may be a result of an increase in its chief food plant (*Passiflora incarnata* L.) in its winter range. After devastating freezes in 1983 and 1989, many citrus groves in central Florida were left fallow and became more favorable for *P. incarnata*. Similarly, the occurrence of more winter nectar sources in fallow groves might account for the near-significant increases in spring migrations of *P. sennae*—despite its declining fall migrations.

I have no ready explanation for the declines in both the spring and fall migrations of *J. coenia*. Perhaps greater use of herbicides to obtain weed free lawns contributes. T. C. Emmel (personal communication) reports that the species breeds well on the *Plantago* spp. that are weeds in turf. What does not show in the data from this study is that in the early 1970s the fall *J. coenia* migrations were heavier than any seen since. The only data I have to support this assertion are that polyester traps operated in fall of 1975 recorded a net migration of *J. coenia* 56% as great as that of *P. sennae*, more than three times more than the average of 17% for the traps and years of this study (Walker 1978). Similarly, Edwards and Richman (1977), in a 1975 study of heights of flight during fall migration, observed 44% as many *J. coenia* as *P. sennae*.

The fall migrations of all the principal migrants showed some decline, but the declines of *P. sennae* and *U. proteus* were especially striking. From 1984 to 1989 the mean net southward migration for these two species was 750 and 404. From 1990 to 1999, for the 8 yr with data fully comparable to the earlier period, it was 279 and 62. This amounts to reductions of 63 and 85%. In the case of *U. proteus*, no migration was recorded after fall 1996, when 25 were trapped flying southward and one was trapped flying northward. In 1997, none was trapped during the 17-d period during which 23% of their migration had occurred in earlier years. No data were available for 1998, but in fall 1999 only three were caught, of which one was flying northward.

The significance of the decline in numbers trapped hinges on whether the catches of migrants in one 6-m flight trap is representative of butterfly migration into and out of the Florida peninsula. I will address this question at three levels. At the lowest level, the question is whether the catches are representative of the trapping site. Here the answer is an easy yes, because the catches of the #3 trap and its companion trap were closely correlated ( $r^2 = 0.95-0.98$ ). This refutes the hypothesis that the #3 trap was becoming poorer and poorer at catching migrants for some idiosyncratic, undetected reason.

At an intermediate level, the question becomes whether migrations at the trapping site were typical of migrations in the immediate vicinity of Gainesville. An

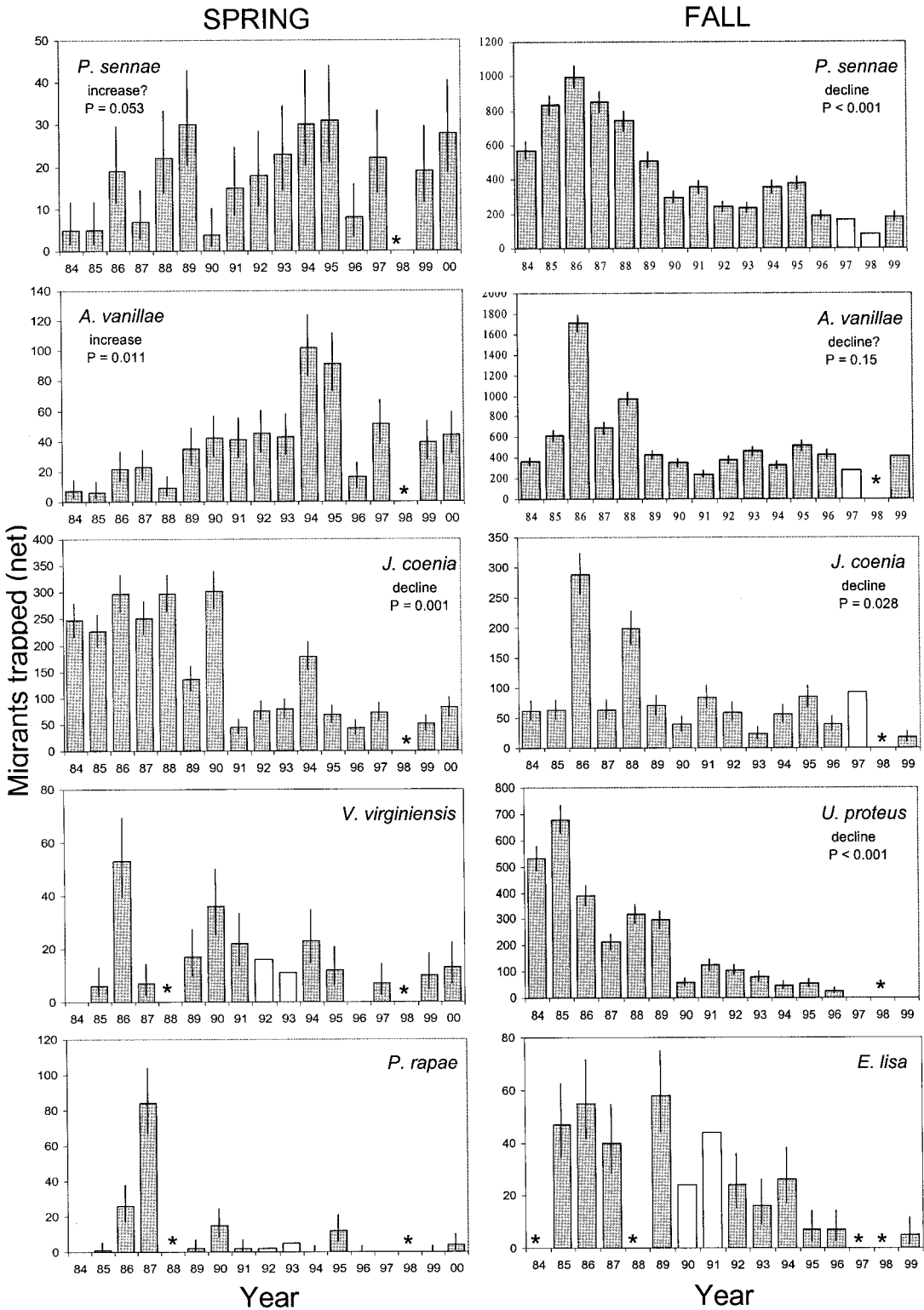


Fig. 4. Annual numbers of spring and fall migrants as estimated by traps near Gainesville, FL. Open bars are estimates (see text). An asterisk (\*) indicates no data and no estimate. Error bars are 95% confidence intervals. P values are for the regression of log net number of migrants on year for the four principal migrants. Numbers of migrants were not adjusted for trapping efficiencies, estimated at 49–70% for *P. sennae*, 22–50% for *A. vanillae*, and 38–60% for *U. proteus* (Walker 1985b).

early experiment is relevant here. In 1975, I simultaneously flight-trapped migrants at sites 4 km west and 11 km east of the site of the current study, and the catches of the most numerous migrants were not significantly different (Table 3, Walker 1978). More to the point, but less quantitative, repeated observations of the fall migrations in the Gainesville area indicate that the migrants are everywhere in similar numbers rather than concentrated in defined corridors. I first observed the fall migrations of *P. sennae*, *A. vanillae*, *J. coenia*, and *U. proteus* through Gainesville in the early 1960s, and the magnitude and dependability of these migrations were what prompted me to start their study. Trap catches were always correlated, at least roughly, with observations of migration intensity throughout the Gainesville area (e.g., Walker 1985a, Walker and Littell 1994). My casual observations of migration intensity became more frequent in late 1990 when I occupied an office that had a clear, ground-level view across a lawn to the east (10 km ESE of the trapping site). Here I watched migrants fly by, or not, whenever I looked up. After ending flight trapping in fall 1997, because the trapping seemed to be yielding nothing new, I resumed it in spring 1999, because the numbers of migrants seen from my office in fall 1998 were far fewer than ever before. In fact, I estimated that the fall 1998 migration of *P. sennae* could not have been more than half of the previous lowest migration (Fig. 4).

At the highest level, the question becomes whether the migrations at the trapping site were representative of a line extending from coast to coast across north peninsular Florida. Here the observations of Barbara Lenczewski (1992) are uniquely relevant. During the falls of 1986, 1987, and 1988, she counted *P. sennae* and *A. vanillae* as she drove, and butterflies crossed, a 192-km transect from Crescent Beach on the Atlantic coast to Steinatchee on the Gulf coast. She drove the transect two to four times per year and after adjusting the raw counts for time of day and time of season, she established migration profiles for nine transect segments across the state for each year. Using the median of the annual values, she produced a generalized migration profile for the transect for each of the two species. On this basis she estimated that the average migration density of *P. sennae* and *A. vanillae* along the transect was 1.00 and 1.47 times the density at Gainesville in the vicinity of the study site. Thus, the decline in numbers of migrants captured by the flight traps in this study probably reflects a decline of similar proportions in the major butterfly migrations in and out of the Florida peninsula.

The most likely cause of the large, sustained declines in the fall migrations of *U. proteus* and *P. sennae* is a decrease in their food plants in source areas. The principal food plants of *U. proteus* are various beans, among which the soybean (*Glycine max* Merr.) is by far the most abundantly available. For example, 2,100,000 acres (8,502 km<sup>2</sup>) were planted to soybeans in Georgia in 1984 (NASS 1999). The area devoted to soybean cultivation has declined greatly in recent years. In Georgia, a probable source of many of the

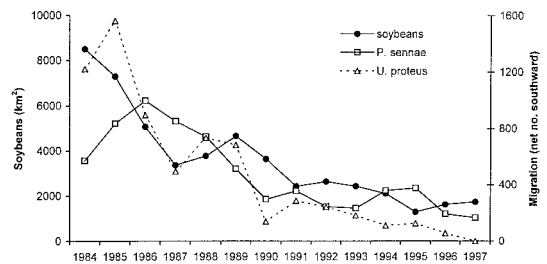


Fig. 5. Fall migration of *P. sennae* and *U. proteus*, 1984–1997, through north peninsular Florida, compared with area planted to soybeans in Georgia. (Net numbers of migrant *U. proteus* multiplied by 2.3 to scale them to those of *P. sennae*.)

migrants, plantings dropped 81% between 1984 and 1998 (NASS 1999) (Fig. 5). The fall migrations of *P. sennae* may also reflect the reduced planting of soybeans. *Cassia obtusifolius* (L.) is both a common weed in soybean fields and a favored food plant of *P. sennae*. In the remaining soybean fields, *C. obtusifolius* may have been reduced by increased use of glyphosate herbicides in conjunction with the planting of transgenic, glyphosate-resistant soybeans. These herbicide-resistant soybeans, first available in 1996, accounted for 72% of United States soybean acreage in 1999 (Monsanto 1999).

The decline in the *P. sennae* migrations should be compared with an anticipated decline in the migrations of *D. plexippus*. Brower and Malcolm (1991) concluded that the migrations of monarchs to overwintering sites in Mexico, where millions aggregate, are in danger of extinction even though the species *D. plexippus* is not. The threat to the migrations is mainly from increasing destruction and degradation of Mexico's oyamel forest ecosystem, which monarchs depend on for favorable microclimates during their winter dormancy (Brower et al. 2000). The numbers of monarchs migrating into Mexico each fall have been variously estimated. For example, Taylor (2000), using explicit assumptions, estimated that fall migrants during 1998 and 1999 numbered >147 million and fewer than 400 million. The numbers of *P. sennae* migrating into Florida each fall averaged an estimated 43 million during 1984–1988 ( $22.2 \times 1.00 \times 1.92$ ) (Walker 1991, Lenczewski 1992). Although *P. sennae* probably had far fewer fall migrants than monarchs have, the *P. sennae* migrants funneled into the relatively narrow Florida peninsula rather than flying on a much broader front from the United States into Mexico. Furthermore, *P. sennae* are individually more visible during migratory flight, because they are bright yellow and because they fly near the ground rather than exploiting upper winds as monarchs do. Thus, the fall flights of *P. sennae* through north peninsular Florida may have been as spectacular as the fall flights of monarchs into Mexico, or even more so. Of importance in this comparison is that monarchs owe much of their migratory fame to another phenomenon—their dense overwintering aggregations in Mexico, between the fall and spring migrations. Monarchs attract additional



attention by flocking during fall migratory flights and by aggregating at nocturnal roosts on the way to Mexico. *P. sennae*, lacking the chemical defenses of monarchs, would not benefit from aggregating.

During fall of 1999, the number of *P. sennae* migrating into Florida was so much lower than previously (<25% of the average for 1984–1988) that the migration was no longer an easily noticed mass movement to the south. The mass fall migrations of *P. sennae* into Florida may be, like the mass aggregations of overwintering monarchs in Mexico, an endangered biological phenomenon (Brower and Malcolm 1991).

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