Butterfly migration from and to peninsular Florida

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Abstract. 1. Migrating butterflies were monitored with traps for 10 years at a site in north peninsular Florida, to determine seasonal and annual variation in numbers and directions of flight.

2. In the spring, 81–96% of the principal migrants, *Phoebis sennae* (L.), *Agraulis vanillae* (L.), *Precis coenia* (Hübner) and *Urbanus proteus* (L.), flew northward; in the autumn, 86–95% flew southward.

3. Estimated mean net numbers of these four species flying northward in spring across each ENE–WSW metre were 3, 6, 69 and <1 respectively; numbers flying southward in autumn were 222, 413, 37 and 146.

4. During a 5-year period, the ratio of highest to lowest seasonal migration for a species did not exceed 9.3.

5. The average median date of spring migration was 27 March for *P.sennae*, 23 April for *P.coenia*, and 12 May for *A.vanillae*. The average median date of autumn migration was 2–5 October except for *U.proteus*, whose average date was 14 October.

6. The autumn migratory period, as measured by the duration of the middle half of migration, was about 2 weeks in *P.coenia* and about 4 weeks in the other three species.

7. Compared to previously reported butterfly migrations, the ones studied here were notably uniform in magnitude and regular in timing.

8. These and other data suggest that 4 million or more of these butterflies migrate northward from peninsular Florida almost every spring and that 40 million or more migrate southward to peninsular Florida almost every autumn.

Key words. Migration, orientation, flight traps, phenology, *Phoebis sennae, Agraulis vanillae, Urbanus proteus, Precis coenia.*

Introduction

Unlike most other insect migrants, migrating butterflies usually fly near the ground and in directions that are largely independent of wind (Williams, 1930; Baker, 1978). Their numbers

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are sometimes great enough to attract public attention, and their size and bright colours make them easy to identify and study on the wing. However, with a few exceptions (*Danaus plexippus* (L.) in North America: Urquhart & Urquhart, 1978; Brower, 1985; *Ascia monuste* (L.) in Florida: Nielsen, 1961; *Aglais urticae* L. in Germany: Roer, 1968; *Pieris rapae* (L.) in Britain: Baker, 1984; *Nymphalis californica* Boisduval in California: Shapiro, 1975, 1980),

the routes, destinations and ecological significance of butterfly migrations are poorly understood. This study is part of a continuing effort to describe and explain migrations of butterflies in the southeastern United States.

The most conspicuous butterfly migrants in the southeastern states are *Phoebis sennae* (L.) (Pieridae), *Agraulis vanillae* (L.), *Precis coenia* Hübner (Nymphalidae) and *Urbanus proteus* (L.) (Hesperiidae) (Walker, 1980, 1985a). Each of these species breeds every summer well north of its overwintering range and can be observed every autumn flying southward toward peninsular Florida. In the eastern United States, *A.vanillae* and *U.proteus* overwinter only in southern Florida. The overwintering areas of the other two species include southern Georgia and Mississippi.

From 1975 to 1978, for periods of 1 year or less, portable flight traps of polyester mosquito netting were used to monitor butterfly migrations at Gainesville, in north peninsular Florida (Walker, 1978, 1980). These traps proved inefficient and prone to wind and sun damage. Beginning in 1979, a series of permanent traps, made principally of hardware cloth, were built and tested. These required no maintenance, and the better models caught 35–60% of the migrants intercepted (Walker, 1985b). This paper uses 10 years of data from these traps to define annual and seasonal patterns of migration and annual variation in numbers of migrants, and to estimate the magnitude of butterfly migration out of and into peninsular Florida each spring and autumn.

Methods

From March 1979 to December 1988, one or two 6 m linear flight traps that intercepted butterflies flying within *c.* 3 m of the ground were operated in a pasture (82°27'19" W lat., 29°40'22" N long.) near Gainesville. Migrating butterflies that encountered a trap's central barrier (a wall of hardware cloth) attempted to continue their linear track by flying over the barrier and thereby entered a duct that led them through valves into holding cages (Walker, 1985b). The traps were built along an ENE–WSW line, approximately perpendicular to the mean direction of migration at Gainesville (Walker, 1985a). Butterflies encountering the traps from the south (actually 158±90°) and from the north (338±90°) were led to separate cages, permitting estimation of net movement northward or southward across the 6 m ENE–WSW line monitored by a trap.

Table 1 details the seasons of service and positions of the five traps used in this study. Traps 1–4 were described and illustrated elsewhere (Walker, 1985b). Trap 5 was made by hanging a 0.3 m wide piece of 13 mm mesh hardware cloth from the eaves of Trap 4, thereby deterring

Table 1. Flight traps (nos. 1–5) used to monitor butterfly migration across 6 m segments of a 13.5 m ENE–WSW line for 10 years near Gainesville, Florida.

| Year | West of 6 m of line | | | East of 6 m of line | | |
	Spring*	Summer	Autumn	Spring	Summer	Autumn
1979	1	1	1	–	–	–
1980–82	1	–	1	–	–	–
1983	1	–	1	–	–	2
1984	1	–	1	3	–	3
1985	–	–	4	3	–	3
1986	5	–	5	3	–	3
1987–88	5	5	5	3	3	3

* The spring and autumn migration seasons, as defined by the behaviour of the butterflies (Fig. 2), were 5 March to 3 June and 27 August to 2 December (standard weeks 10–22 and 35–48; Lewis & Taylor, 1967). Summer was the period between spring and autumn. In most years, trapping was started by 1 March, discontinued during summer, resumed by 27 August, and continued until mid or late December.

butterflies from flying out and reducing the height of the trap opening to 3.3 m, the same as Trap 3.

During periods of operation, traps were emptied daily and the numbers and species taken from each holding cage recorded. Captured butterflies were not released in the vicinity of the traps and were sometimes preserved for further study.

Results and Discussion

Spring and autumn migrants

The four conspicuous migrants, *P.sennae*, *A.vanillae*, *P.coenia* and *U.proteus*, made up more than 85% of the total catch and were the only species shown to migrate northward in spring and southward in autumn (Table 2). In spring and in autumn more than 80% of captures of these four species were in the migratory direction.

Five other species totalled more than 100 individuals for either spring or autumn seasons during the 10 years of trapping (Table 2). Two of these, *Pieris rapae* and *Vanessa virginiensis* (Drury), showed significant movement northward in spring (80% and 72% northward) but were seldom caught in autumn, a finding consistent with their overwintering as far north as Canada (Scott, 1986). *Eurema lisa* (Boisduval & LeConte) overwinters throughout the south-

eastern States and extends its range northward into Canada in mid to late summer (Scott, 1986). It showed significant movement southward in autumn (74%) but was never caught in spring. *Eurema daira* (Godart) overwinters in the southeastern Coastal Plain and spreads northward a few hundred kilometres in summer (Scott, 1986). It showed no significant net movement in autumn for all years combined (424 southward *v.* 407 northward), but in 1985 autumn numbers were biased southward (112 *v.* 69; $\chi^2 = 9.75$, $P<0.005$). The remaining species, *Eurema nicippe* (Cramer), overwinters throughout the southeastern States and was the only species that showed a significant net movement in a seemingly inappropriate direction. For all autumns combined, 57% of those captured were flying northward. However, in only three of the five years in which autumn catch exceeded 100 was there a significant net movement northward. In the other two of these years northward captures were 51% and 50% of the autumn totals.

Danaus plexippus, a well-known migrant, often migrates at heights well above those monitored in this study (Gibo, 1986). Nonetheless, enough were trapped to show a significant southward bias in autumn (Table 2). None of the other two species known to migrate southward in autumn through northern Florida, *Panoquina ocola* (Edwards) and *Lerema accius* (Smith) (Walker, 1978, 1980), was caught.

Table 2. Numbers and directions of butterflies captured during spring and autumn migration seasons near Gainesville, Florida, 1979–88. All species are listed for which ≥100 were captured in either the spring or autumn migration season. *Danaus plexippus* is listed because it is a well known migrant.

Species	Spring				Autumn			
	N	S	%N	*P**	S	N	%S	*P**
Phoebis sennae	137	6	96	<0.001	9145	782	92	<0.001
Agraulis vanillae	156	7	96	<0.001	9273	345	96	<0.001
Precis coenia	3126	266	92	<0.001	1646	275	86	<0.001
Urbanus proteus	13	3	81	<0.05	3982	217	95	<0.001
Eurema nicippe	13	8	62	NS	1101	1436	43	<0.001
Eurema lisa	0	0	–	–	531	189	74	<0.001
Eurema daira	3	1	75	NS	424	407	51	NS
Pieris rapae	155	38	80	<0.001	3	8	27	NS
Vanessa virginiensis	130	51	72	<0.001	5	4	56	NS
Danaus plexippus	0	1	0	–	13	2	87	<0.01

* Chi-square test of no. northward = no. southward. Note that *E.nicippe* is biased northward in autumn.

These skippers are too small to be deflected into the catching cages by 13 mm mesh hardware cloth.

Annual pattern of captures, directionality and migration

For three of the principal migrants, *P.sennae*,

A.vanillae and *U.proteus*, less than 2% of captures were in spring and more than 90% were in autumn (Fig. 1). For *P.coenia*, spring captures were 58% of the total and autumn captures were only 40%. For none of the four species did summer captures exceed 8%. The weeks with greatest catches for each of the four species (Fig. 1) were the weeks with the most highly
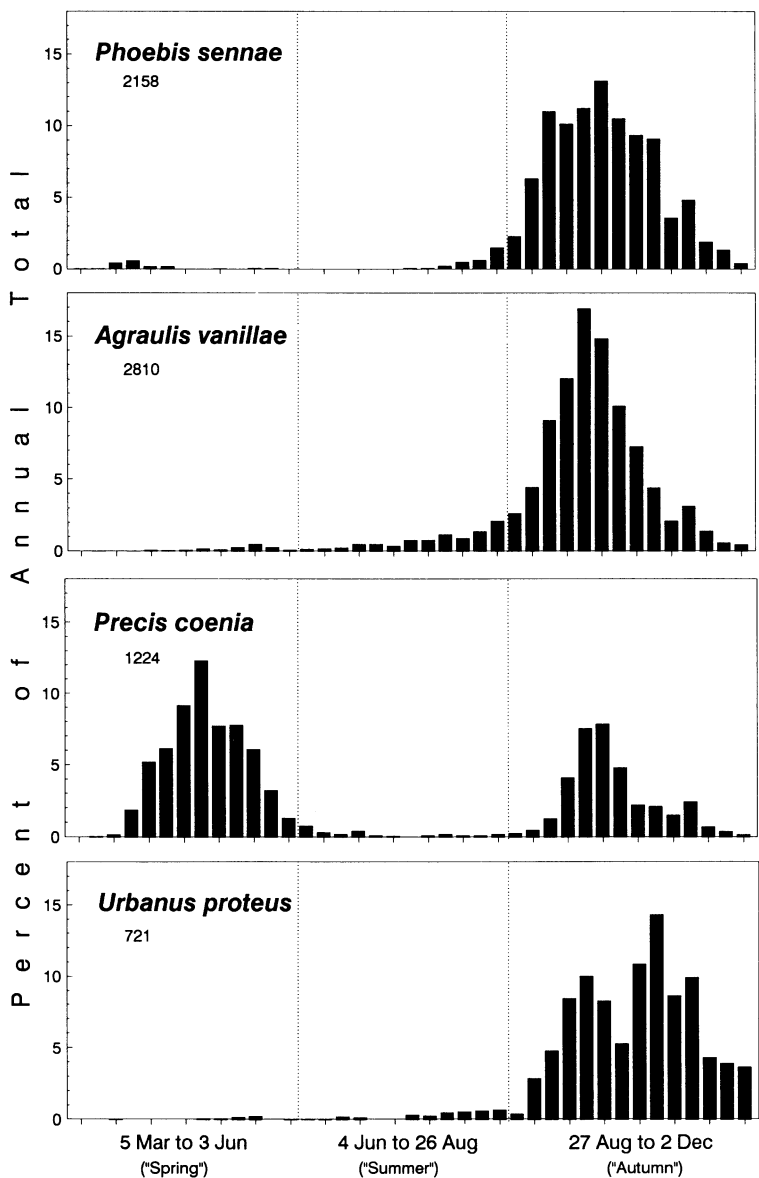
Fig. 1. Weekly rates of captures for principal migrants during 1986–88 (Traps 3 and 5). Mean weekly catch is graphed as per cent of mean annual catch, which was calculated by summing the means for each season and is listed beneath each species name. Dotted lines separate seasons (Table 1 footnote).
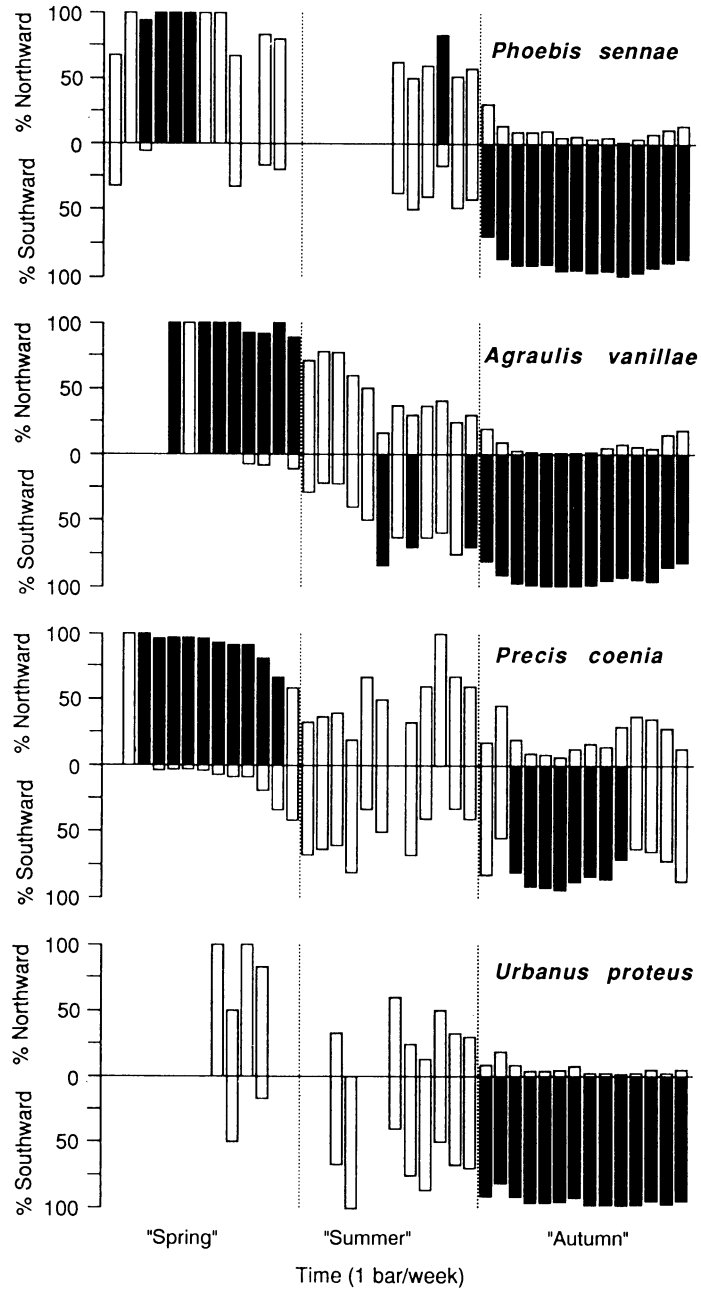
Fig. 2. Seasonal changes in directions of flight for principal migrants during 1986—88 (Traps 3 and 5). If direction of flight was significantly biased (chi-square $P<0.05$) during a week, bar is filled in direction of bias. Weeks with $n=0$ or 1 are omitted. (See Fig. 1 for relative sample sizes and Table 1 for trapping schedule.) Dotted lines separate seasons.

biased flight directions (Fig. 2). Strong north-ward bias was maintained in spring until about the first week in June — though the numbers were often too low for statistical significance. Numbers of individuals trapped and directional biases remained low during most of the summer. Then, during the last week in August, south-ward bias became strong in three of the species and remained so into December (Fig. 2). In *Precis coenia*, strong southward bias began about 2 weeks later and markedly diminished by early November.

Because directional biases were consistently high during migratory seasons, fluctuations during spring and autumn in net numbers of each principal migrant matched fluctuations in total numbers caught (Fig. 1). (Net number is the number flying in the migratory direction minus the number flying in the opposite direction.) Seasonal timing of migration is detailed in Fig. 3, which shows average dates for completion of the first, second and third quartiles of net movement northward in spring and south-ward in autumn. It also shows 95% confidence intervals about the mean midpoints of migration and the annual variation in completion of the first and third quartiles of migration.

In spring, *P.sennae* migrated first, followed by *P.coenia* and *A.vanillae*, with the mean mid-points of migration being 27 March, 22 April and 12 May respectively (Fig. 3A). Based on thirteen northward captures, *U.proteus* re-sembled *A. vanillae* in the timing of its northward spring movement. Sequence of spring migration correlates with winter range: the overwintering areas of *P.sennae* and *P.coenia* include north peninsular Florida, whereas the two late-flying species usually overwinter only in south Florida (Walker, 1978; Scott, 1986).

In autumn, the four principal species migrated nearly synchronously; and, except in *P.coenia*, the migration lasted longer than in spring (as measured by the duration of the middle 50%) (Fig. 3B). Mean date of the migration midpoint was 2 October for *P.coenia*, 5 October for *P.sennae* and *A.vanillae*, and 14 October for *U.proteus*. Timing of autumn migration was far more variable in *U.proteus* than in the other species, with the migration midpoint being as early as 25 September (1987) and as late as 16 October (1985). The extended period of autumn migration for the four principal species suggests that north of Gainesville individuals

continue to mature and emigrate rather than emerging and emigrating synchronously.

Annual variation in numbers of migrants

Because Traps 1, 3 and 5 were operated for 3–6 years in the same place and manner, the annual variation in net numbers caught flying northward in spring or southward in autumn by each of these traps measured year-to-year variation in numbers of migrants. Although the traps were of different design, their catches were made comparable by adjusting for trap-ping efficiencies (Figs 4 and 5). For 1979–83 the migrations were monitored only by Trap 1, which caught almost no *U.proteus* and c. 1–10% of the other species. Consequently seasonal totals were often too small to justify estimates of year-to-year variation in relative numbers. On the other hand, for 1984–88, migrations were monitored with one or two traps that were c. 35–60% efficient.

For the five years with data from efficient traps, the ratio of highest to lowest seasonal migration for a species did not exceed 9.3 (Figs 4 and 5). In the three cases with adequate data for 10 years, only for *P.coenia* in spring did the ratio exceed an order of magnitude. The year-to-year uniformity of the migrations monitored in this study contrasts with extreme annual fluctuations reported for many species (e.g. *Vanessa cardui* (L.) Myres, 1985; *Libytheana bachmannii* (Kirkland), Gilbert, 1985). This may be due in part to the fact that without traps that operate continuously or a massive mi-gration, monitoring butterfly flights is dull work. Consequently massive migrations (unlikely to occur yearly) are studied and contrasted with years in which migration is lacking (or so sparse as to go unnoticed). The migrations here documented are modest enough to have long gone largely unnoticed and entirely unstudied. Shapiro (1980, 1986) postulated similarly thin seasonal movements for fifteen species (in-cluding *P.coenia*) to and from altitudes above 1500 m in the Sierra Nevada of California.

Total numbers of migrants

The autumn migratory front spans the Florida peninsula (>170 km), but the traps in this study monitored only 6 m each. Estimating the total number of migrants flying south across the lati-
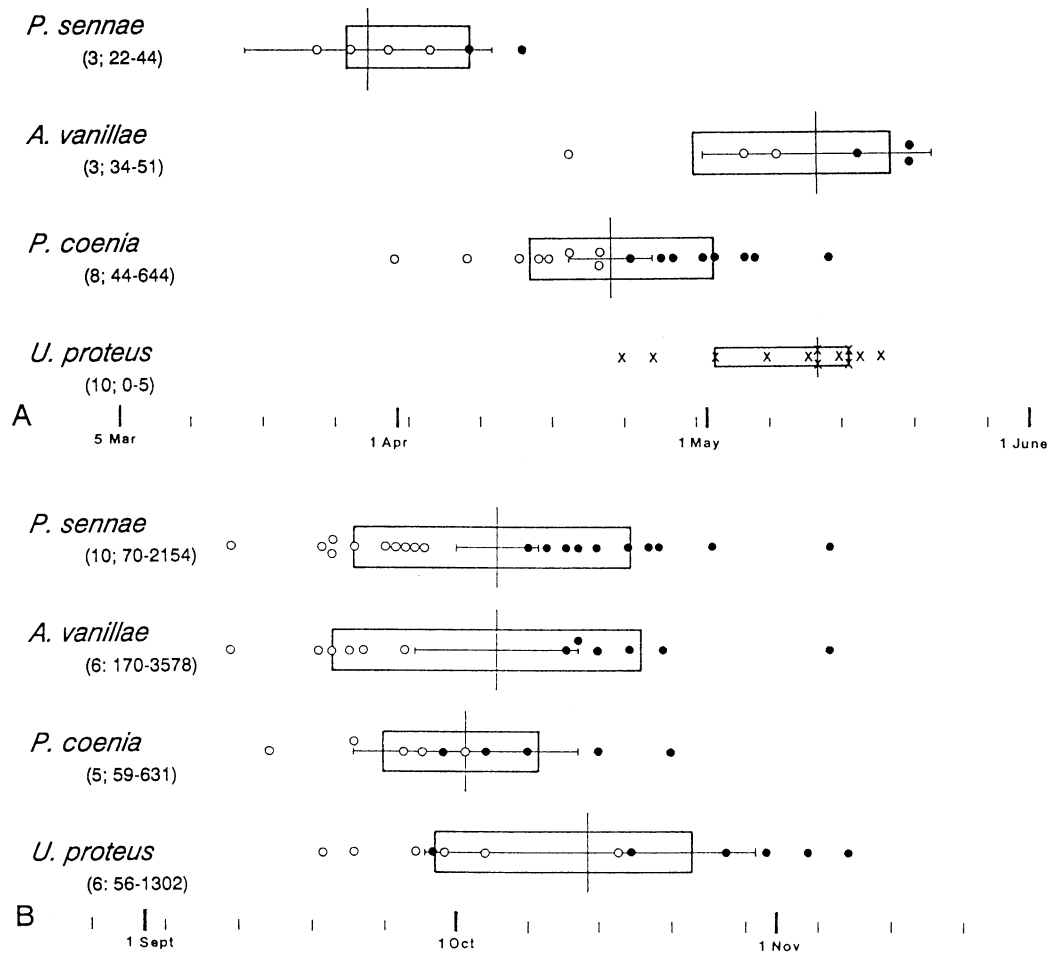
Fig. 3. Timing of spring and autumn migration of principal migrants. Vertical lines are average median dates of migration. Horizontal lines show 95% confidence intervals for median dates. Boxes indicate the middle half of migration (i.e. the period between average completion of first and third quartiles of net movement in the migratory direction). Open dots show annual variation in completion of first quartile; filled dots show annual variation in completion of third quartile. Number of years and range of annual numbers of migrants used for quartiles are in parentheses beneath each species name. Thin ticks on time scales are first days of standard weeks. (A) Spring migration. For the first three species, years with net spring captures of <20 were excluded. For *U.proteus*, all individuals captured flying northward in spring are indicated by ×'s (*n*=13), and quartiles are based on the pooled sample rather than on annual data sets. (B) Autumn migration. Years with net captures of <50 were excluded.

tude of Gainesville depends on knowing how the migration at the trap site compares with the average migration across the latitude. During the autumns of 1986, 1987 and 1988, B. Lenczewski monitored *P.sennae* and *A.vanillae* along a cross-Florida transect that passed through Gainesville. Her counts indicated that

the average rate of migration across the transect was no less than 60% of the rate at the longitude of the trapping site (personal communication). Thus I estimated the total migration of these two species to peninsular Florida (and the other two by inference) by assuming that the rate of migration at the traps occurs across 100 km
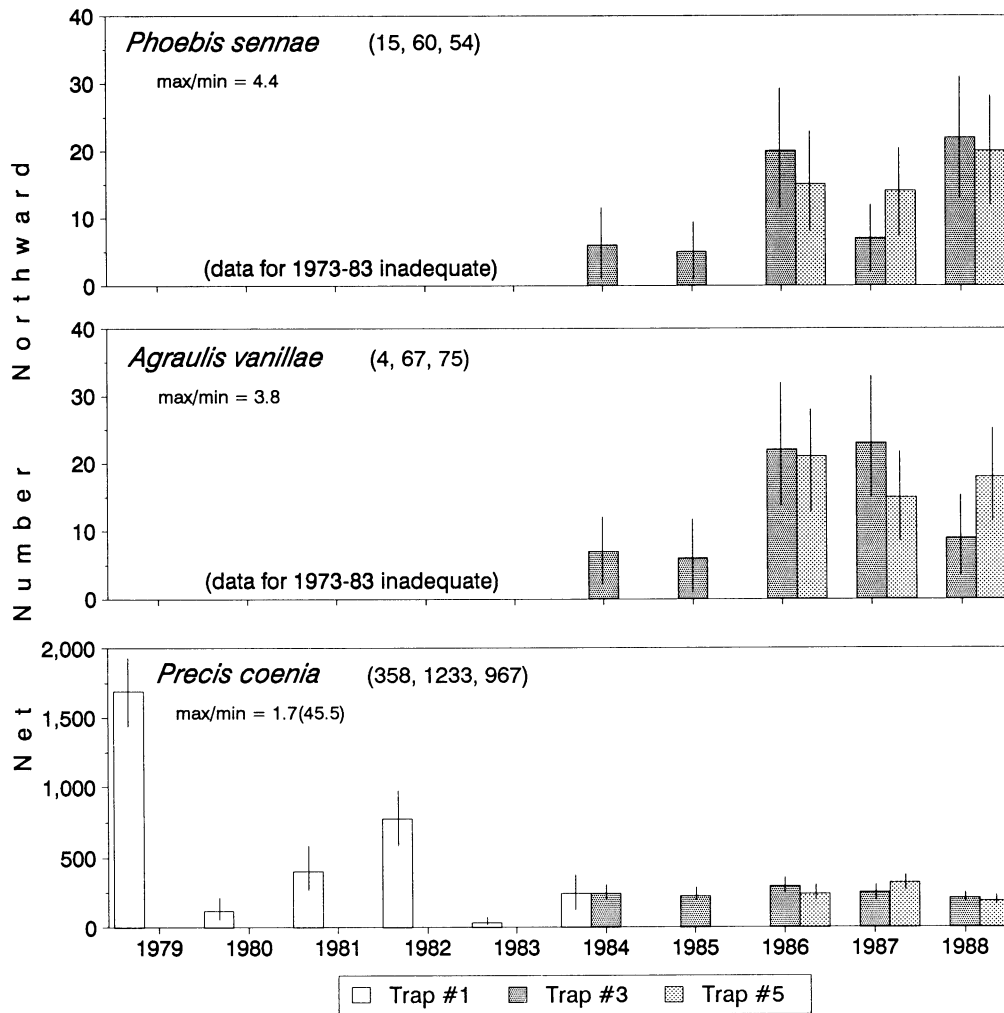
Fig. 4. Annual variation in net movement northward in spring for principal migrants. Numbers for Traps 1 and 5 are adjusted for trap efficiency to be directly comparable to those for Trap 3. Error bars are 95% confidence limits based on Poisson distribution. (Three numbers after species names are total net numbers caught by Traps 1, 3 and 5 respectively — before adjustments for efficiency.) No data are plotted for Trap 1 when its 1979—84 net catch of a species totalled <30. The ratio of highest to lowest seasonal migration was calculated for each species for 1984—88 (and for 1979—88 if data were adequate).

(Table 3). In the absence of other data, I estimated spring migration from the Florida peninsula based on the same assumption.

Although each trap used in this study spanned 6 m of migratory front, none was fully efficient. Trapping efficiency of Trap 3 for autumn migrating *P.sennae* was earlier estimated as 60% (95% c.i.=49—70%), for *A.vanillae* 35%

(22—50%) and for *U.proteus* 49% (38—60%) (Walker, 1985b). These efficiencies can be used to convert estimates based directly on catches of Trap 3 to estimates of absolute numbers (Table 3). (Because trap efficiency for *P.coenia* was unknown, it was assigned the highest efficiency measured among the other three species.)
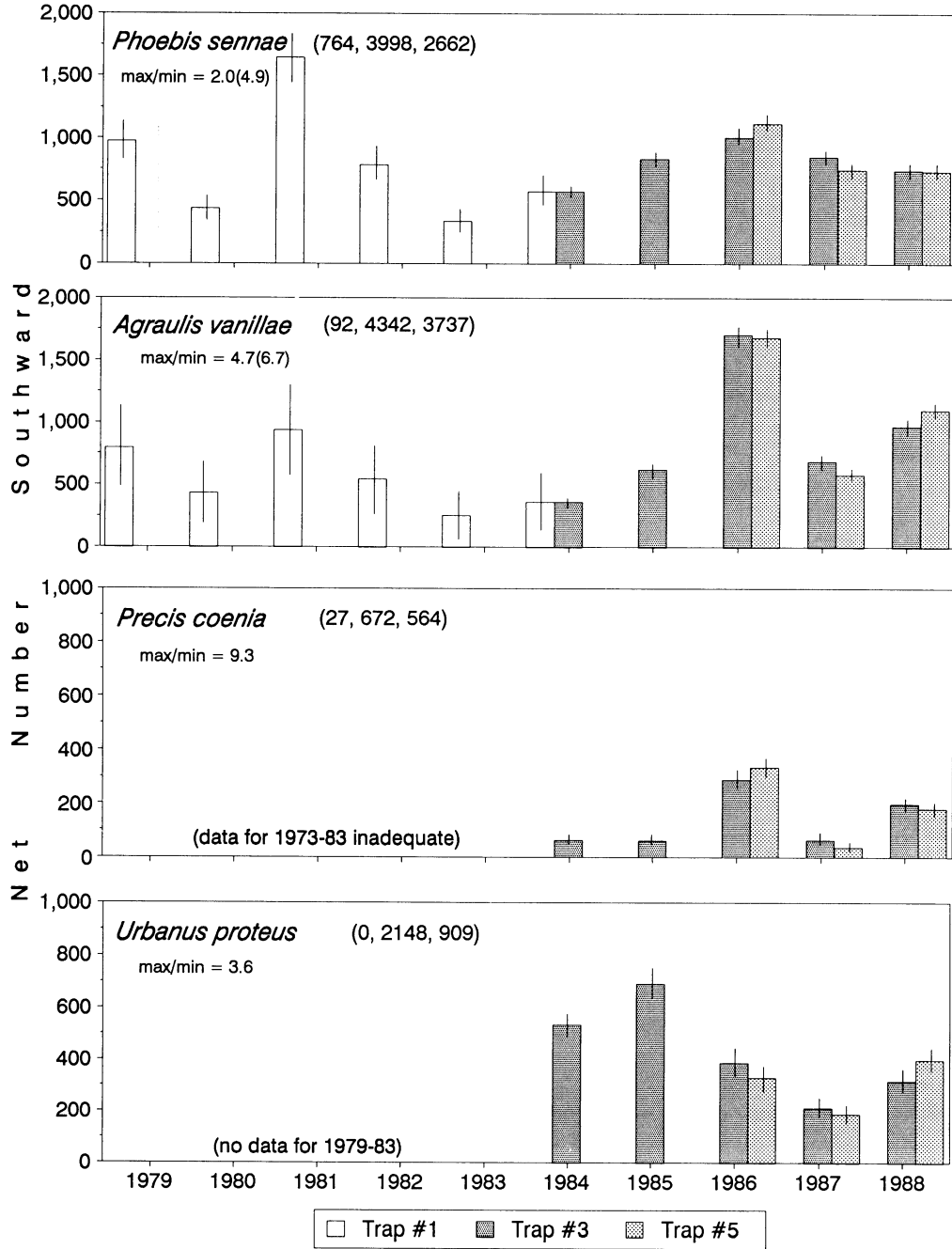
Fig. 5. Annual variation in net movement southward in autumn for principal migrants. See Fig. 4 for explanation of numbers and bars.

Table 3. Estimates of average annual absolute numbers of principal migrants flying from and to the Florida peninsula. Numbers caught by Trap 3 are for 1984–88; efficiencies are from Walker (1985b). The remaining two columns of numbers extrapolate the results of trapping to a migratory front of 100 km (see text).

Species	Trap 3 (6 m) ($\bar{x}\pm95\%$ c.i.)	No./100 km (millions)	Efficiency (%)	Adj. no./100 km (millions)
Spring migration				
Phoebis sennae	12±9	0.2	60	0.3
Agraulis vanillae	13±9	0.2	35	0.6
Precis coenia	247±42	4.1	60*	6.9
Sum	272±39	4.5		7.8
Autumn migration				
Phoebis sennae	800±220	13.3	60	22.2
Agraulis vanillae	868±647	14.5	35	41.3
Precis coenia	134±141	2.2	60*	3.7
Urbanus proteus	430±234	7.2	49	14.6
Sum	2232±46	37.2		81.8

* In the absence of data, *P.coenia* is assigned the highest estimated efficiency.

Based on the above reasoning, total spring migration is estimated to average *c*. 8 million and total autumn migration is estimated to average *c*. 80 million (Table 3). Trying to assign confidence intervals to these estimates seems futile, but confidence limits (based on Student's *t*) are easily calculated for the average seasonal net catches of Trap 3. It is noteworthy that these limits for total seasonal net catches are less, relative to the mean, than the confidence limits for seasonal means of the individual species (Table 3). This stems from lack of synchrony in the annual variations in migration of the four species (Figs 4 and 5). Indeed, the range of values obtained by dividing the five yearly seasonal totals by the 5-year average is 0.9–1.2 for spring and 0.7–1.5 for the autumn. Thus it seems safe to predict that whatever the absolute average seasonal totals are, the total migration for either spring or autumn will seldom be less than half or more than double the long-term seasonal average.

General discussion

This study differs from all previous long-term studies of butterfly migration in that traps allowed continuous, objective monitoring of migrants. Consequently migrations that were 'thin' to 'very thin' (Williams, 1930, p. 321) were detected and reliably quantified. Four species proved to migrate north in spring and south in autumn, although the spring migration of *U.proteus* was too scant to demonstrate a significant northward bias in any one year. These four species apparently breed well north of where they can overwinter (Walker, 1978; Scott, 1986), making southward movement in autumn the only way that many individuals can retain a chance to contribute to the next year's gene pool. However, *P.sennae* and *P.coenia* need not migrate as far south as peninsular Florida to find a survivable winter climate, suggesting that southern or central Florida has other advantages to autumn migrants — such as more food, fewer enemies, or an opportunity for additional generations. The northward movement of the four species in spring leads to summer reproductive success as evidenced by the numbers of autumn migrants.

Even in autumn, the numbers migrating per day are small compared to most butterfly flights reported in the literature (e.g. Williams, 1930); however, the migration occurs for so many hours for so many days over such a wide front that the total number flying southward through north peninsular Florida each autumn is similar to the number of *D.plexippus* that are estimated to overwinter in spectacular aggregations at a few

sites in the mountains of the Transvolcanic Belt of Mexico (Brower & Calvert, 1985; Calvert & Brower, 1986). That the Florida migrants do not aggregate in winter may be attributed to Florida's lack of cool mountains to lower their metabolic rates, as well as to their greater susceptibility to predators compared to car-denolide-laced monarchs. The autumn migrants that reach peninsular Florida may or may not breed during the winter. In southern Florida, some winter reproduction apparently occurs in all four species, but it is uncertain whether the breeders are autumn migrants or permanent residents (B. Lenczewski, personal communication; M. K. Hennessey, personal communication).

Not only is it uncertain exactly what autumn migrants do during winter, it is not known exactly where they go to do it. B. Lenczewski (personal communication) has discovered that migration generally stops north of Lake Okeechobee. The area between Gainesville and Lake Okeechobee is large enough (*c.* 51,600 km^2) that 81.2 million butterflies would be scarcely noticeable, if evenly distributed (*c.* 16 per ha).

How migrants orient and whether they navigate are other unresolved problems. Compass orientation, by sun or other means, has ample precedence in insects; but navigation does not. The evidence for navigation is that migrants in West Florida, Georgia and South Carolina take different, appropriate headings toward peninsular Florida (Walker, 1985a, and unpublished).

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