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MIGRATION AND RE-MIGRATION OF BUTTERFLIES THROUGH NORTH PENINSULAR FLORIDA: QUANTIFICATION WITH MALAISE TRAPS[1]

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ABSTRACT. Malaise traps with single linear barriers perpendicular or parallel to the axis of the Florida peninsula were operated from 18 Sept. 1975 to 17 Sept. 1976 near Gainesville; insects intercepted by the two surfaces of each barrier were captured separately allowing them to be scored as flying northward, southward, eastward, or westward. During the fall, significantly more individuals were caught flying southward than northward for eight species of butterflies: *Urbanus proteus* (Linnaeus); *Phoebis sennae* (Linnaeus); *Precis coenia* (Hubner); *Panoquina ocola* (Edwards); *Agraulis vanillae* (Linnaeus); *Lerema accius* (Smith); *Urbanus dorantes* (Stoll); and *Eurema lisa* Boisduval and Le Conte. Estimated net numbers flying southward across each meter ranged from 3956 (*U. proteus*) to 33 (*E. lisa*). During the spring significantly more individuals were caught flying northward than southward for two species: *P. coenia, A. vanillae.* Estimated net numbers were 150 and 10 per m, respectively. Malaise traps can continuously and effectively monitor insect migration within the boundary layer.

Long-distance flights by insects are frequent and of theoretical and practical interest (Williams, 1958; Johnson, 1969; Dingle, 1972). Such movements are difficult to study because quantification requires identifying flying insects and determining their directions of movement as well as counting them. Most long-distance flights of insects may occur at night or at high altitudes making detailed observations impractical, although mass flights above 10 m can be studied with radar (Schaefer, 1976; Riley, 1975). Direct visual observation is useful for large insects that fly low in daylight. Butterflies have been the most frequent subjects of such observations (Arbogast, 1966; Baker, 1968b; Balciunas and Knopf, 1977). Since direct observation is difficult and time consuming, the resulting data are generally skimpy and likely to be biased by choice of observation times.

Malaise traps (Southwood, 1966) can complement direct observation of flights of low flying insects by continuously sampling without the presence or bias of an observer. Appropriately modified, a Malaise trap can separate insects flying in one direction when intercepted from those flying in another direction. I used four such traps to monitor insect flights within 2 m of the ground for one year near Gainesville, Florida.

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[1] Florida Agricultural Experiment Station Journal Series No. 457.

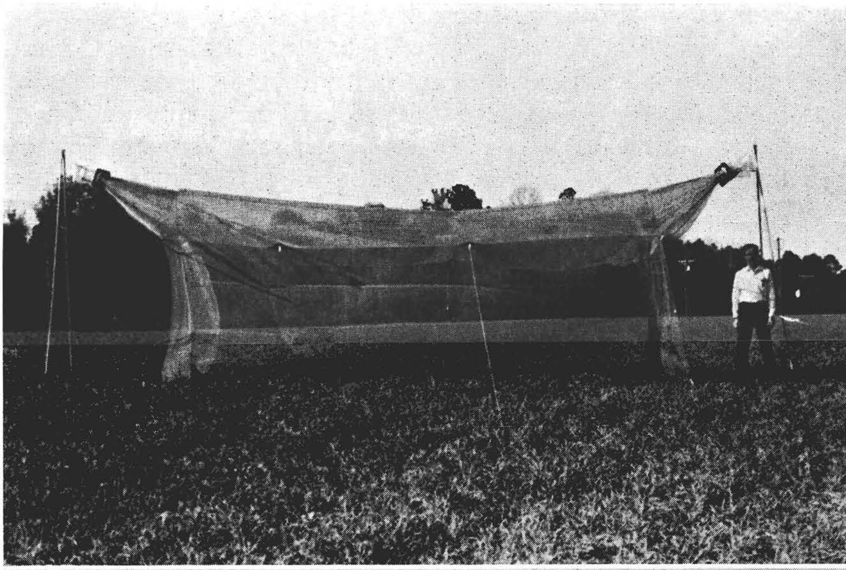

Fig. 1 (above). N–S trap at Green Acres site, looking NNW.
Fig. 2 (below). Heads at one end of trap, showing how insects from the two sides of the barrier were kept separate.

METHODS

Special Malaise traps (Fig. 1) were constructed and are now commercially available.[2] Each trap had a 2.6 × 6 m central barrier. Insects flew into the trap by either of two 2 × 6 m openings that faced in opposite

[2] D. A. Focks & Co., P. O. Box 12852, University Station, Gainesville, Fla. 32604.

directions. Upon striking the central barrier they sometimes worked their ways toward either end, through a truncated funnel, and into a receptacle where they were killed by vapors from pieces of dichlorvos-impregnated plastic.[3] Traps were made so that insects entering through one opening remained separated from those entering through the other opening (Fig. 2). The receptacles were emptied daily or two or three times per week depending on the numbers caught. Insects caught within the trap but not present in the receptacles were killed and added to the appropriate batch.

Mating status of samples of female migrants was determined by dissecting for spermatophores.

Traps were set at two sites, 15 km apart: (1) Green Acres Farm, Agronomy Dept., U. of Fla., 18 Sept.–18 Oct. 1975 (4 traps); 19 Oct.–2 Nov. 1975 (2 traps); 10 Apr.–6 June 1976 (2 traps); (2) Archer Road Laboratory, Entomology and Nematology Dept., U. of Fla. 19 Oct. 1975–17 Sept. 1976 (2 traps). The first site was an open field with no buildings or woods within 100 m (Fig. 1). The second was a lawn-like area with buildings 50 m to the west and east. Traps were set in pairs with one member of each pair oriented WSW–ENE (perpendicular to the axis of the Florida peninsula and to the predicted track of migrants—henceforth called a N–S trap) and the other (an E–W trap), 30 m away, NNW–SSE (parallel to the axis of the Florida peninsula and at right angles to the N–S trap).

The insect-catching devices (heads) of the traps were improved during the first month of the study by changing the receptacles from translucent polypropylene jars to transparent bags (Fig. 2). Even with improved heads, a trap captured only a small portion of the insects that flew over the 6-meter line defined by its barrier. The efficiency of traps was estimated from counts of individuals captured versus individuals evading capture during observation periods (4, 5, 12, and 26 Oct., 1975).

RESULTS

For eight species of butterflies the N–S traps caught significantly more individuals flying southward than flying northward in the fall (Table 1). For two of the eight, N–S traps caught significantly more individuals flying northward than flying southward in the spring.

Estimating net numbers moving southward (or northward) each week or each season requires not only counts of individuals caught but also an estimate of trapping efficiency. During the four observation periods to determine efficiency of N–S traps with improved heads, 28 of 314 *Urbanus*

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[3] e.g. 3 × 6 cm pieces of No Pest or Stable Strip, Shell Chemical Co.

TABLE 1. Numbers of individuals trapped flying northward and southward and estimated net displacement[1] (in parentheses) during four seasons, 18 Sept. 1975–17 Sept. 1976, near Gainesville, Fla.

	"Fall" 26 Aug.–26 Nov.[2]			"Winter" 27 Nov.–25 Feb.			"Spring" 26 Feb.–26 May			"Summer" 27 May–25 Aug.		
	N	S	(net/m)[1]	N	S	(net/m)	N	S	(net/m)	N	S	(net/m)
U. proteus	38	2453[3]	(3956)	4	5		0	1		3	1	(3)
P. coenia	17	178[3]	(312)	2	5	(2)	155[4]	45	(150)	4	4	
P. sennae	10	244[3]	(368)	0	2	(3)	2	0	(4)	0	1	
P. ocola	1	164[3]	(210)	0	0		1	1		0	0	
A. vanillae	0	93[3]	(127)	0	0		11[4]	2	(10)	5	2	(4)
L. accius	9	54[3]	(74)	0	0		3	0	(2)	0	0	
U. dorantes	15	46[3]	(41)	0	0		0	0		0	0	
E. lisa	2	17[3]	(33)	0	0		0	0		0	0	

[1] Estimated number moving in one direction across a 1-m WSW–ENE line in excess of those moving in opposite direction. These estimates do not correlate perfectly with numbers trapped because they take into account number of traps operating and whether original or improved heads were in use (see text).
[2] 18 Sept.–26 Nov. 1975, 26 Aug.–17 Sept. 1976.
[3] Significantly more flying southward than northward ($P < 0.05$).
[4] Significantly more flying northward than southward ($P < 0.05$).

proteus (8.9%) were captured. The efficiency for single observation periods varied from 2 to 12%: 3 of 28 (11%), 19 of 159 (12%), 2 of 88 (2%), 4 of 39 (10%). The lowest efficiency (2%) occurred when the wind was mainly from the north and the skippers were flying higher than usual: 70% flew over the trap without first hitting the barrier compared to 38–43% for the other three periods. So few of the other species were flying that no reliable estimate of capture efficiency was obtained. During the four observation periods 2 of 8 *Precis coenia* were captured, 0 of 7 *Phoebis sennae*, and 0 of 3 *Agraulis vanillae*. None of these ratios differ significantly from the 8.9% observed for *U. proteus* (chi square, $P > 0.05$). To simplify calculation of estimates of net displacement (Table 1 and Fig. 3) while keeping well within the limits suggested by the data on trapping efficiency, I assumed that each trap with improved heads captured 10% of the individuals flying over its 6-m line. For N–S traps with original heads, I assumed a 2.5% efficiency, since when operated simultaneously with N–S traps with improved heads their catches were approximately one-fourth as great (e.g. 115 compared to 469 *U. proteus*). Conversion to improved heads was completed 17 Oct. 1975.

E–W traps caught approximately the same number of insects flying eastward as flying westward. The only significant exception ($P < 0.05$) was for *U. proteus*; 432 were caught in eastward flight versus 177 in westward flight (=2.4:1) during 18 Sept.–17 Nov. Such a bias would be expected if the average track of southbound migrants was east of SSE (158°), the orientation of the central barrier of E–W traps. Balciunas and Knopf (1977) determined that the mean track was 147°—i.e., 11° east of SSE.

Beginning 2 Nov. counts of individuals caught in each end of all traps were recorded separately. The north and south ends of E–W traps showed approximately the same biases as the north and south sides of N–S traps. For example, of the 144 *U. proteus* trapped 2–17 Nov. in one E–W trap, 137 were caught in the south end. (Data from E–W traps were never used in estimating net displacement northward or southward.) The fall flights lasted for six weeks or longer (Fig. 3). The continuous nature of the fall

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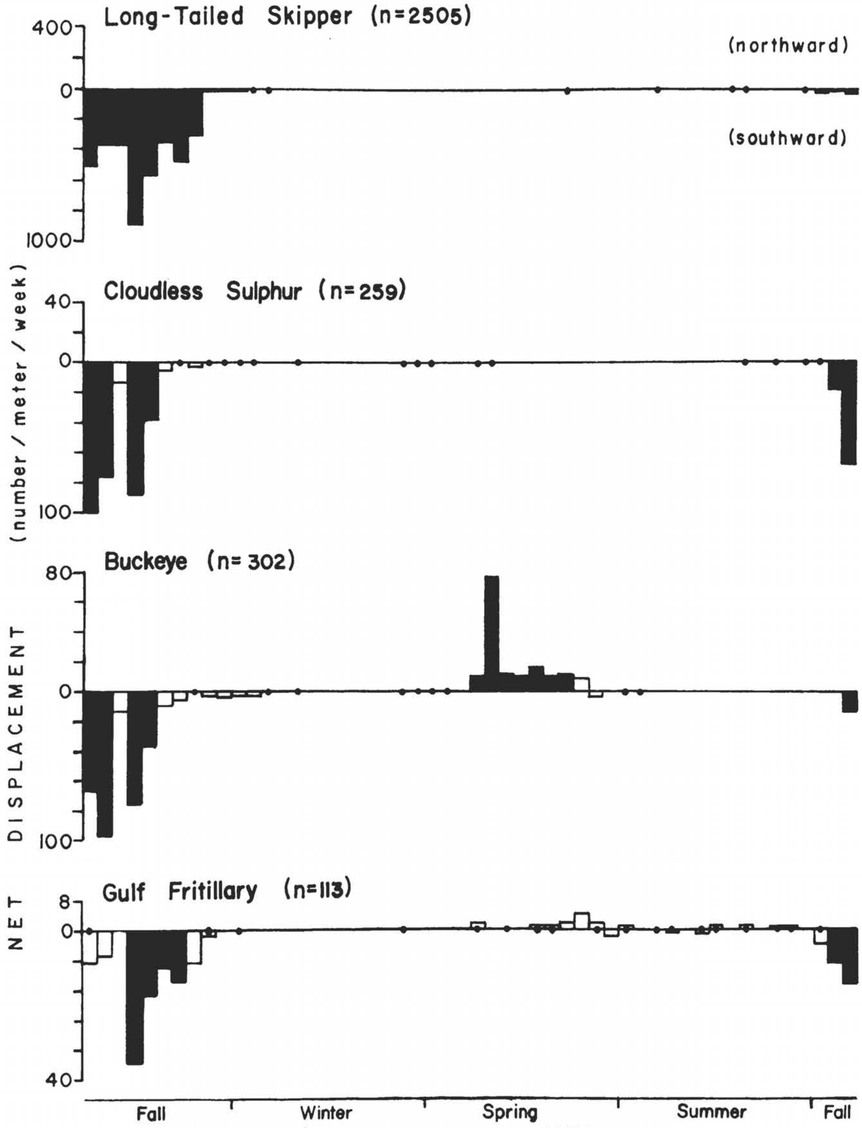
Fig. 3. (Top to bottom) *U. proteus, P. sennae, P. coenia, A. vanillae.* Weekly occurrence and net displacement northward or southward 18 Sept. 1975 through 17 Sept. 1976. Downward bars show net displacement southward; upward bars show net displacement northward. Solid bars indicate a significant ($P \leqslant 0.05$) inequality in numbers caught flying northward and southward. The lengths of the bars show the estimated numbers of individuals flying southward (or northward) across 1 m perpendicular to the axis of the Florida peninsula in excess of those flying in the other direction. Estimates were made from the numbers caught in 1 or 2 N–S traps. Traps



with original heads (18 Sept.–16 Oct. 1975) were assumed to be 2.5% efficient; traps with improved heads (11 Oct. 1975–17 Sept. 1976) were assumed to be 10% efficient (see text). Since the final "week" had 9 days (9–17 Sept.), its estimates were multiplied by 7/9 prior to plotting. Bars without dots indicate weeks in which numbers caught flying north and south differed by more than one (N–S traps). Dots indicate other weeks in which at least one individual was caught (all traps). Bars with dots (gulf fritillary only) indicate one individual caught flying north or south that week. Dates for seasons are as in Table 1.

TABLE 2. Sex ratios during fall and spring flights and mating status of females.

Species	Dates	Individuals Sexed	Sex Ratio (M/F)	Females Dissected	Percent Mated
U. proteus	9 Oct.–19 Nov.	926	.72[1]	298	21
P. sennae	9 Oct.–19 Nov.	86	.87	37	35
P. coenia	9 Oct.–19 Nov.	116	1.11	42	64
	21 Mar.–14 May	94	2.20[2]	30	80
P. ocola	9 Oct.–19 Nov.	90	1.00	39	62
A. vanillae	9 Oct.–19 Nov.	53	.66	26	77
	5 Apr.–14 May	7	.40	5	100

[1] Significantly different from 1.00 ($P < 0.05$).
[2] Significantly different from 1.00 and from 1.11 ($P < 0.05$).

flights is not adequately documented in Fig. 3. The small numbers caught prior to changing to improved heads exaggerated the fluctuations during the first four weeks. Only for *U. proteus* were sample sizes large enough during this period to give acceptable precision to estimates of net displacement. The day-to-day continuity of the southward flights of *U. proteus* is revealed by the occurrence of such flights on each of the 52 days that the traps were operated between 18 Sept. and 12 Nov. (Storms blew down all traps on the other 4 days during this period.) The smallest one-day catch was 5 (1 flying northward and 4 southward) and the greatest was 149 (1 and 148 respectively).

Males and females participated in fall and spring flights. With two exceptions the sex ratios of migrants did not differ significantly from 1.00 (M/F): Females were significantly in excess of males for *U. proteus* in the fall, and males were significantly in excess of females for *Precis coenia* in the spring (Table 2). Percent of females that had mated varied with the season and species from 21 to 100 (Table 2). Mated females generally contained mature eggs.

DISCUSSION

The Flights

The questions of where trapped individuals of the eight species listed in Table 1 came from, where they would have gone, and what they would have done once there cannot be answered from the results of this study or of earlier studies of one or more of the species (e.g., Williams, 1958; Arbogast, 1966; Urquhart and Urquhart, 1976; Richman and Edwards, 1976; Correale and Crocker, 1976; Balciunas and Knopf, 1977; and Edwards and Richman, 1977). Clues to the answers are provided by the following information on northern limits and overwintering stages (Howe, 1975; Klots, 1951).

Urbanus proteus (Linneaus) (Pyrginae) occurs northward to Connecticut and Arkansas and is not known to overwinter in the U.S. except in Florida (Howe, 1975). In this study significant southward displacement ceased by late November, yet adults remained abundant about the flowers of *Bidens pilosa* Linneaus until a hard freeze occurred 19 Dec. The next ones seen were three individuals, trapped 3 May, 10 June, and 19 July. Greene (1971) reported that adults were seldom seen at Sanford, Fla. (140 km SE of Gainesville) from 1 Jan. to 1 July during 1967, 1968, and 1969.

Precis coenia (Hubner) (Nymphalidae) occurs northward to Wisconsin, southern Ontario, and New England. Gorlick (in Howe, 1975) stated that "adults hibernate in winter," but did not indicate how far northward such hibernation is known. In this study adults were trapped during December and February but none was seen or trapped during January nor for the 104 days between 3 June and 16 Sept. 1976.

Phoebis sennae (Linneaus) (Pieridae) occurs north to Canada but is not known to overwinter in U.S. except in the Gulf region and Florida. Adults are seen in Gainesville throughout the winter (though none was trapped during January 1976; cf. *Precis coenis*). The two specimens captured in N–S traps during spring 1976 were flying northward. None was trapped or seen between 31 Mar. and 28 July.

Panoquina ocola (Edwards) (Hesperiinae) occurs northward to Arkansas and New Jersey. None was trapped between 16 Dec. and 8 Mar.; 6 were trapped from 8 Mar. through 10 May; none between 10 May and 3 Sept.

Agraulis vanillae (Linnaeus) (Heliconiidae) occurs northward to Wisconsin (Schwehr, 1971). No stage survives the winters in Kansas (Randolph, 1927). After the 19 Dec. 1975 freeze in Gainesville, no adults were seen or trapped until 12 Feb.

Lerema accius (Smith) (Hesperiinae) occurs northward to New England and Illinois. During this study the only records were fall catches (5 Sept.–17 Nov.).

Urbanus dorantes (Stoll) (Pyrginae) is common in southern Texas and the Greater Antilles but only recently (1969?) became established in Florida (Knudson, 1974). The Florida population belongs to the Texas rather than to either of the Antillean subspecies (Miller and Miller, 1970); adults occur all winter in South Florida; in the Gainesville area the only records are fall (18 Sept. to 18 Nov.).

Eurema lisa Boisduval and Le Conte (Pieridae) occurs northward to Quebec and Ontario. Neither adults nor pupae seem to survive the winters north of 40° (Howe, 1975). When adults appear in Missouri in late spring, they are "invariably ragged, faded and torn, indicating that they may have flown into the area from the south. In the absence of near freezing temperatures (such as in [south] Florida) there are continuous broods" (Howe, 1975:372). All records during this study were in fall (3 Sept.–26 Oct.).

The information above is compatible with the hypothesis that each of the eight species detected moving southward through Gainesville in the fall breeds farther north than it overwinters. Except for *P. coenis* and *P. sennae*, nothing conflicts with and some data support the more extreme hypothesis that overwintering occurs no farther north than peninsular Florida. Either hypothesis requires northward flights in spring or early summer. The Malaise traps detected such flights only for *P. coenia* and *A. vanillae*. Williams (1958) reported direct observations of northward spring flights for three of the eight species: *P. sennae* (Ala.); *A. vanillae* (Fla.) and perhaps *U. proteus* (Fla.). (The other five species are less conspicuous and/or more difficult to identify on the wing.) The lack of trapping evidence for northward flights in six of the species might be attributed to fewer individuals taking part or to different patterns of flight (e.g. slower and less unidirectional, Nielson, 1960; or above 2 m).

The flights through Gainesville that were documented by Malaise traps differ significantly from the migratory flights of most insects (Johnson, 1969) and perhaps of most butterflies (Baker, 1968a, 1968b, 1969).

Johnson (1969) emphasized that most long-distance flights by insects are above the *boundary layer*—the layer of air near the ground in which the air movement is less than the insect's air speed—and cites instances where long-range dispersal of butterflies may be primarily wind determined. The thickness of the boundary layer depends on air speed of the insect, speed of the wind, and degree to which the roughness of terrain or vegetation slows the air near the ground. The butterflies and skippers observed during this study and captured in the Malaise traps were generally, probably always, flying within their boundary layers. When the wind was blowing in the direction of flight, the migrants flew higher, and when the wind was blowing counter to the direction of flight, they flew lower, but butterflies and skippers were never seen flying at wind speeds greater than their air speeds. When the flights were greatest, the winds were light and variable. Air speeds for *A. vanillae* average 18 km/h (Arbogast, 1966) while those for *U. proteus*, *P. coenia*, and *P. sennae* average 23, 18, and 20 km/h respectively (Correale and Crocker, 1976; Balciunas and Knopf, 1977). Flight heights for the same four species (over open ground) are generally 0.2–2.0 m (Arbogast, 1966; Edwards and Richmond, 1977).

Baker (1968c, 1968b, 1969) concluded that at least six and possibly eight of nine species of British migratory butterflies for which he had data orient by means of the sun but do not compensate for its movements. In other words, mean flight direction during the day changes approximately 15°/hr. Such is not the case for the four species that have been studied at Gainesville. Arbogast (1966) found no significant shift in flight direction with time of day for *A. vanillae* nor did Balciunas and Knopf (1977) for *U. proteus*. I have similar unpublished observations for *P. coenia* and *P. sennae*. By what means these insects maintain approximately the same compass direction at all times of day is unknown. Two hypotheses seem especially worth testing: time-compensated sun orientation (e.g. Frisch, 1974) and orientation by means of the earth's magnetic field (e.g. Lindauer, 1977). Malaise-type traps could be used to capture large numbers of migrants for clock-shifting experiments or for testing with simulated suns or magnetic fields.

Since the Malaise traps operated continuously and collected small, plain insects as well as large, showy ones, they had the potential of detecting migratory flights of species that were rare, inconspicuous, or difficult to identify on the wing. Four of the eight species detected migrating (Table 1) were such species: *P. ocola*, *L. accius*, *U. dorantes*, and *E. lisa*. The methods of trapping and of analyzing the catches could have detected boundary-layer migratory flights of species in other insect groups—for example, moths, flies, wasps, and dragonflies. None was detected although low-altitude directional flights of such insects have been observed elsewhere (Williams, 1958). Species of these groups either did not migrate through Gainesville at altitudes below 2 m or they migrated in numbers too small to be detected by one or two 6-m Malaise traps.

The Method

The estimated net displacements northward and southward in Table 1 and Fig. 3 should be evaluated as to precision (repeatability) and accuracy (correspondence to true value). Different N–S traps at the same site or at sites 15 km apart gave estimates of net displacement that were so similar that the traps could not be proved different with the number of paired observations available (Table 3). The only apparent problem with precision is variation in trapping efficiency attributable to wind direction (see above).

Evaluating accuracy depends on comparing the values obtained with Malaise traps with values obtained by using other methods. Since no other method of continuous or automatic monitoring has been developed, the only comparisons that can be made are with direct, visual observations. The only such observations made were brief and not intended to check

TABLE 3. Comparisons of effectiveness of two N–S traps in detecting net displacement when they were 43 m apart at the same site (Green Acres) and when they were at two sites 15 km apart.

Comparison Species (season)	Number of Observations[4]	Net Numbers[1] Trap A $\bar{x} \pm SD$[2]	Trap B $\bar{x} \pm SD$[2]	Accept H_0[3]
Same site				
U. proteus (fall)	16	15.2 ± 20.4	11.2 ± 11.4	yes
Different sites				
U. proteus (fall)	11	34.9 ± 20.4	42.4 ± 25.8	yes
P. coenia (spring)	5	7.6 ± 1.8	5.4 ± 2.8	yes

[1] In fall, number intercepted flying southward less number intercepted flying northward; in spring, the reverse.
[2] Standard deviation is used here merely as a measure of variation; distribution of catches was not assumed to be normal.
[3] The null hypothesis (H_0) was that traps A and B were sampling the same population with equal effectiveness. The Wilcoxon Matched-Pairs Signed-Ranks test at P = 0.05 was used (Siegel, 1956).
[4] Number of days (*U. proteus*) or weeks (*P. coenia*) during which both traps were operative and at least one individual was caught. For the observations of *P. coenia* no period shorter than a week could be used because trap-service dates at the two sites generally coincided but once per week.

the accuracy of trapping estimates; however, the two methods of estimation agree well enough (Table 4) to suggest that the error in trapping estimates of the four species directly observed is decidedly less than an order of magnitude. For *U. proteus* this evaluation has an element of circularity because direct observation of that species yielded the 10% trapping efficiency that is incorporated into the formula for estmating net displacement from trapping results.

Advantages of using Malaise traps to study migration within the boundary layer include the following: (1) Continual monitoring is practical. (2) Sensitivity is great enough to detect small-scale flights. (3) Cost is low enough to permit replication or extensive montoring. (4) Acceptable precision and accuracy are attainable. (5) Capture of individuals permits positive identification and determination of sex and mating status. (6) With modified heads, traps could catch large numbers of individuals for mark-release studies of destination of migrants or for studies of means of orientation.

The following are important limitations to using Malaise traps in studying insect migration (though some can be overcome by modifying the trap design): (1) Only flights near the ground can be monitored (modified traps could be suspended from tethered weather balloons). (2) Traps are damaged by severe storms (hardware cloth or woven wire could be substituted for the polyester mosquito netting). (3) Information as to flight direction is crude: ± 90° (traps with barriers every 90° or 45° could be built). (4) Weather factors, such as wind direction, will affect

TABLE 4. Comparison of estimates of numbers flying southward across a 1 m WSW–ENE line, per hour, by direct observation and by trapping at Green Acres site.

Species	Method of Estimate	Date and Time of Direct Observation 11 Oct. 1975 1552–1622	12 Oct. 1975 1248–1318	26 Oct. 1975 1229–1252
U. proteus	Direct[1]	20.5	27.7	16.0
	Trapping[2]	15.0	23.2	7.7
P. coenia	Direct[3]	1.3	1.6	0.9
	Trapping[2]	3.5	5.4	0.4
P. sennae	Direct[3]	1.8	0.4	0.5
	Trapping[2]	0.7	2.1	0.4
A. vanillae	Direct[3]	0.3	0.4	0.7
	Trapping[2]	0.5	0.5	0.2

[1] Based on counting individuals crossing a 6 m WSW–ENE line.
[2] Based on the day's catch of individuals in N–S traps with improved heads. Trapping efficiency was assumed to be 10% and flight activity was assumed to be spread evenly over 7 hrs: indiv/m/hr = 10N/w/7, where N is number trapped flying southward and w is width of trap(s) (6 m for 11 and 12 Oct.; 12 m for 26 Oct.).
[3] Based on counting individuals crossing a 15 m WSW–ENE line.

height of flight and hence trapping efficiency. (5) An insect entering the trap from one direction may have a greater probability of beng captured than one entering from another direction. For example once an insect has struck the barrier, it may fly toward the brightest light—often the sun to the south. If the direction of attempted escape is south, an insect on the south side of the barrier would be more likely to escape than one on the north side of the barrier. If this bias occurs, it is apparently slight: For example, *Hylephila phyleus* (Drury), (Hesperiinae), was caught in larger numbers than any other nonmigratory skipper or butterfly. Of 198 individuals caught in N–S traps, 111 were captured on the north side and 87 on the south side. A chi square test reveals no significant bias ($P > 0.05$).

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