

**MIGRATING LEPIDOPTERA:
ARE BUTTERFLIES BETTER THAN MOTHS?***

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A significant number of species of insects, especially Lepidoptera,¹ breed each summer hundreds of kilometers farther poleward than they overwinter. Individuals must therefore be making the sort of long-distance, habitat-to-habitat movements that entomologists generally term *migration*. This paper examines the annual migration to higher latitudes of certain butterflies and moths, and particularly the occurrence or nonoccurrence of return flights by the progeny or grandprogeny of the individuals that flew poleward.

SUBJECT SPECIES

Ten species, 5 butterflies and 5 moths, are the principal examples in this paper (Table 1). Each is believed to migrate northward in the eastern United States in spring or summer and to produce 1 or more generations in

TABLE 1. FIVE BUTTERFLIES AND 5 MOTHS THAT ANNUALLY SPREAD NORTHWARD IN THE EASTERN UNITED STATES AND BREED IN AREAS UNSUITABLE FOR OVERWINTERING.

Species	Reference
Butterflies	
Monarch	<i>Danaus plexippus</i> (Danaiidae) Urquhart and Urquhart 1979
Cloudless sulphur	<i>Phoebis sennae</i> (Pieridae) Walker 1978
Buckeye	<i>Precis coenia</i> (Nymphalidae) Walker 1978
Gulf fritillary	<i>Agraulis vanillae</i> (Heliconidae) Walker 1978
Bean leafroller	<i>Urbanus proteus</i> (Hesperiidae) Walker 1978
Moths*	
Fall armyworm	<i>Spodoptera frugiperda</i> Snow and Copeland 1969
Velvetbean caterpillar	<i>Anticarsia gemmatalis</i> Buschman et al. 1977
Cabbage looper	<i>Trichoplusia ni</i> Chalfant et al. 1974
Soybean looper	<i>Pseudoplusia includens</i> Mitchell et al. 1975
Beet armyworm	<i>Spodoptera exigua</i> Mitchell 1979

*All are Noctuidae.

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¹This and subsequent superscript numbers refer to notes in the appendix, p. 93.

areas farther north than overwintering can occur. It should be emphasized that evidence for individuals of a particular species *not* overwintering at any particular northern latitude is always less than perfect.² Nonetheless, all indications support the conclusion that the 10 species in Table 1 breed each summer much farther north in eastern United States than they overwinter. For the monarch and the fall armyworm the northward seasonal spread has been mapped (Baker 1978: 426; Snow and Copeland 1969); the former reaches Canada by late May while the latter apparently arrives 2 months later.³

The 5 moths in Table 1 are major pests, and 1 of the butterflies (*U. proteus*) is a minor pest. Long distance movements of Lepidoptera, in the eastern United States and elsewhere, are of more than academic interest.

MODELS OF MIGRATION

If one concedes that various species of North American Lepidoptera regularly breed in areas far to the north of where they can overwinter, a number of models may be used to accommodate the phenomenon. Three (Fig. 1) are of special interest:

Diffusion and freeze-back (Fig. 1a). Each spring the extent of suitable habitats enlarges northward, reaching a maximum by midsummer. Wandering, ovipositing females that happen to travel northward find unexploited, productive habitats. The cumulative effect of random movements is a diffusion-like net movement toward higher latitudes. Long distance unidirectional flights are not involved; the rapidity and extent of spread depend on the amount of "trivial" movement per female and the number of generations during spring and summer. In fall, when cold weather moves southward, the populations at higher latitudes are successively extinguished, and the winter range is approximately the same as the year before.

Relieve population pressure (Fig. 1b). In spring, conditions in the overwintering area become favorable and populations rapidly increase. At some threshold density, individuals (of the proper ontogenetic stage—perhaps newly eclosed adults) emigrate. The emigrants may simply fly upward and be carried in whatever direction the upper air is blowing. One result of emigration is that the overwintering habitat is not destroyed by excessively dense populations; another is that the emigrating individuals are carried to unsuitable habitats (e.g. Atlantic Ocean or xeric grasslands) or to (temporarily) suitable ones (e.g. summer breeding areas in the North). As the populations build up in summer breeding areas, more emigration ensues. When fall arrives, breeding slows or ceases and the range contracts to its winter extent because of cold-induced deaths at higher latitudes. The principal difference between this and the previous model is that individuals engage in long distance, unidirectional⁴ flights in response to high density. Northward spread is rapid, not because all or most emigrants go that direction but simply because those that do, go far.

The first 2 models present an evolutionary dilemma⁵ that is clearest in the second: In the relieve-population-pressure model, those individuals that unselfishly emigrate are not as well represented in the next overwintering population as those that stay. Any genetic variation toward staying would have a selective advantage over 1 for emigrating. In the diffusion-freeze-back model all individuals are presumed to behave the same, but again, any

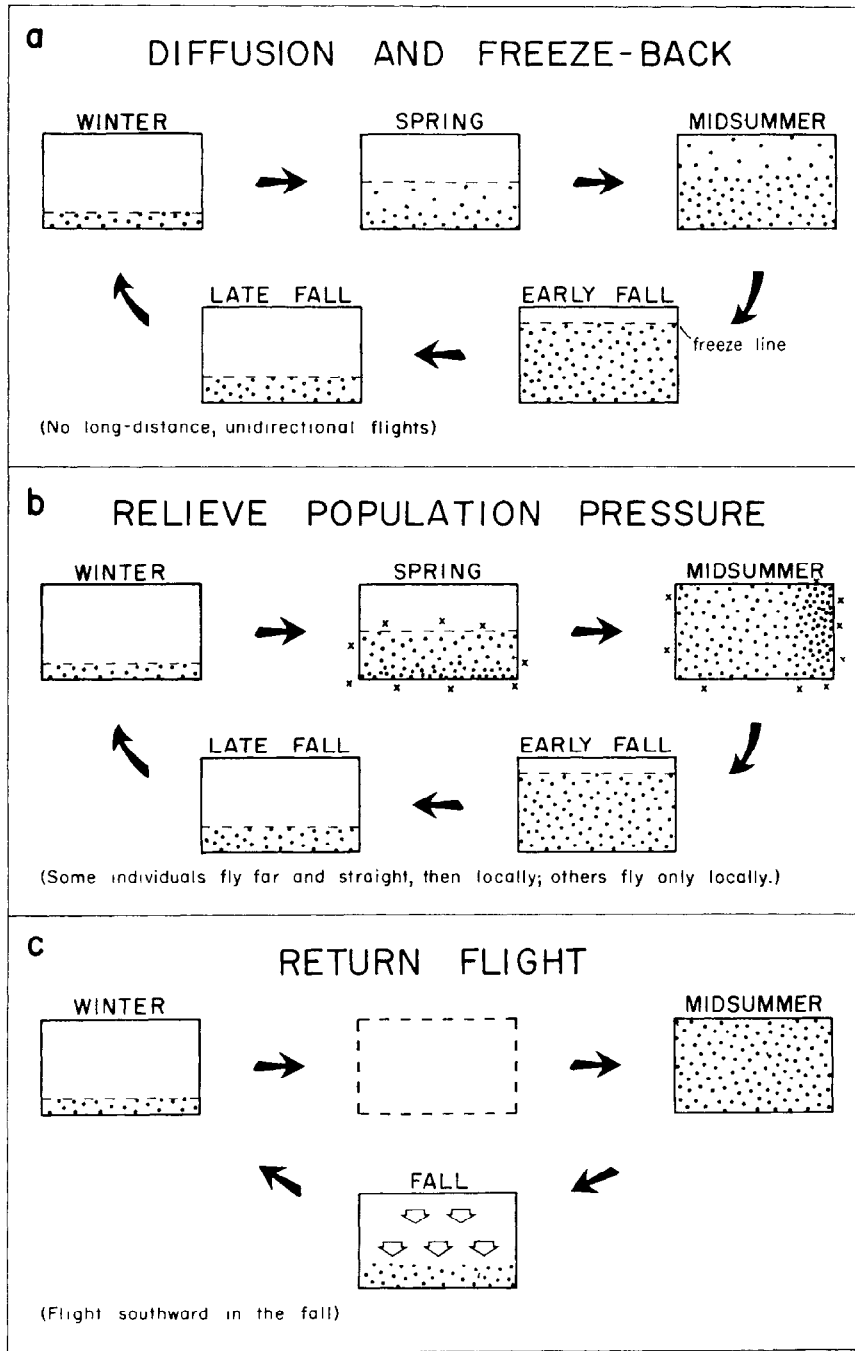


Fig. 1, a-c. Three models that account for species annually breeding at higher latitudes than they overwinter. (Upward is poleward.) (See text for further explanation.)

genetic variation toward moving only short distances and avoiding poleward movement would be favored. Each successive overwintering population should have lesser frequencies of whatever genes promote spread into areas where progeny or grandprogeny perish in the fall.

Return flight (Fig. 1c). In this model there is no evolutionary dilemma because the genes that move northward in spring and summer return southward in fall. The overwintering population includes not only genes from those that stayed the previous spring but also from those that moved northward. This model is not specifically concerned with the means of northward movement (hence the blank rectangle in Fig. 1c), but it is noteworthy that once a return flight is postulated, moving straight northward into the summer breeding area should often increase reproductive success more than movements in other directions.

The evolutionary consequences of 3 alternative behavioral strategies are made explicit in Table 2. The consequences of northward spread with no return trip have already been discussed. The reproductive success of staying compared to that of spreading northward and returning depends upon these factors: (1) the average summertime increase per generation in the overwintering area compared to areas to the north, (2) number of generations during the summer (south and north), and (3) extra mortality resulting from migration. When the reproductive payoffs of the 2 strategies are equal (as in Table 2), neither should replace the other. To some extent the relative payoffs will change depending on the frequencies of the alternative strategies. For example, if only a few individuals remain in the overwintering area during the summer, their rate of increase should equal that of individuals moving northward; and, spared migratory mortality, they should contribute more to the winter population. On the other hand, if only a few individuals move northward, the payoff of staying is reduced and the average increase per generation in the North may be greater—since even after 1 or 2 generations the resources of the summer breeding areas should be largely unexploited. (If, at all frequencies, individuals moving northward fare better than those that stay, that species should cease to breed in the overwintering areas.) The particular values for parameters in the first 3 columns of Table

TABLE 2. EVOLUTIONARY CONSEQUENCES OF 3 GENETICALLY PROGRAMMED ALTERNATIVE STRATEGIES. VALUES ARE HYPOTHETICAL AND ADJUSTED TO MAKE THE FIRST 2 BEHAVIORAL STRATEGIES HAVE EQUIVALENT EFFECTS. SEE TEXT FOR FURTHER EXPLANATION.

Genotype	Average increase per generation*	Increase during summer**	Return trip mortality	Contribution to winter population
Stay	1	1	—	1
Spread northward; return in fall	10	1000	0.999	1
Spread northward; no return	10	1000	—	0

*Populations presumed to hold their own in already-occupied overwintering area and to show rapid increase in newly occupied areas to the north.

**Assuming 3 generations in the North.

2 should vary not only with the frequencies of the alternative strategies but also with weather conditions (south and north) and with numbers of other species (e.g. enemies, competitors, food sources).

The evolutionary forces bearing on staying or moving northward and returning are complex, but genetically based behavioral rules that result in a particular strategy may be fairly simple. The most complicated strategy listed in Table 2 ("Spread northward, return in fall") is well within the range of complexities demonstrated for genetic programming in insects. Table 3 outlines a possible program⁶ and compares it with 1 that occurs in aphids.⁷

Return flights are expected on the basis of evolutionary theory, and their genetic programming is creditable—but do they occur in the 10 species of Table 1? The answer for the 5 species of butterflies apparently is *yes*; for the 5 species of moths no direct evidence of return flights exists. Are butterflies better (at coping with long range movements) than moths?

RETURN FLIGHTS IN BUTTERFLIES

The most convincing evidence for a return flight in butterflies is for the monarch. Since 1938, F. A. Urquhart has headed a program of attaching identifying labels to the wings of monarch butterflies—the equivalent of a banding program for birds. Numerous monarchs tagged in the fall in the North have been recovered along the Gulf coast and in central Mexico (Fig. 2b). (Directional flights northeastward in the spring also have been demonstrated; see Fig. 2a.)

The evidence for a return flight in the other 4 subject species of butterflies is the same as the evidence in eastern monarchs prior to Urquhart's tagging program: they are seen flying persistently in appropriate directions

TABLE 3. GENETIC PROGRAMS PRODUCING DIFFERENT PHENOTYPES DEPENDING ON PHOTOPERIOD AND POPULATION DENSITY. THE 1 FOR MOTH OR BUTTERFLY IS SPECULATIVE; THE 1 FOR PARTHENOGENETIC FEMALE APHIDS IS SIMILAR TO A PROGRAM EXPERIMENTALLY VERIFIED FOR THE VETCH APHID (LEES 1961).

Species	Conditions	Phenotype
Moth or butterfly		
	Photoperiod increasing <i>and</i> density at maturity >D	FLY NORTHWARD
	Photoperiod at maturity decreasing >2 min per day	FLY SOUTHWARD
	Otherwise	MAKE NO LONG-DISTANCE FLIGHT
Parthenogenetic female aphid		
	Photoperiod >15 h <i>and</i> density >D	PRODUCE ALATAE
	Photoperiod >15 h <i>and</i> density <D	PRODUCE APTERAE
	Photoperiod <15 h	PRODUCE SEXUAL FORMS

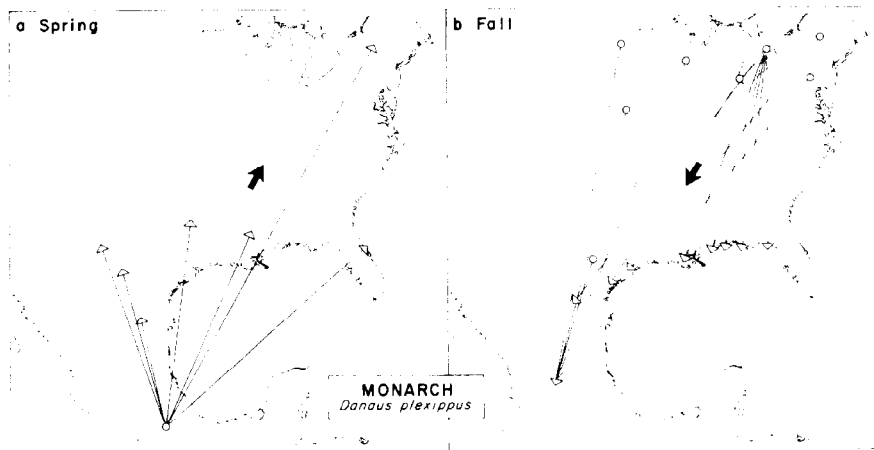


Fig. 2. Recoveries of monarchs tagged in winter (a) and late summer (b). Redrawn from Urquhart and Urquhart (1978, 1979).

in the fall. Fall migratory flights are near the ground—i.e. in the boundary layers—and singularly unidirectional. When a migrating individual comes to an obstacle, such as a house or dense clump of trees, it rises and flies over rather than deviating to the right or to the left. Nearly all individuals maintain approximately the same direction, and the direction is not noticeably influenced by wind or time of day (Fig. 3) (Arbogast 1966, Balciunas and Knopf 1977).

Only the bright yellow, hard-to-ignore cloudless sulphur has been repeatedly observed in fall migration at localities widespread in eastern United States (Fig. 4). Most observations, and all annually repeated ones, indicate a return flight to overwintering areas in the South. The pattern differs from that of the monarch in that most flights are toward the Florida peninsula rather than toward Texas and Mexico.

I have studied the density and seasonal pattern of butterfly migrations at Gainesville using special 2-way flight traps of polyester (Fig. 5a) or hardware cloth (Fig. 5b) (Walker 1978, Walker and Riorden 1980). Southward flights in the fall have been substantiated for 2 or more years for 7 species (Table 4), including 3 that were not detected visually. Estimated numbers varied from nearly 4,000,000/km (bean leafroller, "1975") to about 1,000 (buckeye, 1979). Significant southward movement starts in early September and continues, whenever weather is favorable, into early November (Walker and Riorden 1980).

Flights in the spring were studied with the same traps. Only the buckeye showed significant northward movement during more than 1 year (Table 5), yet such movement must occur in any species that annually reoccupies northern summer breeding areas. Failure to detect it in most species trapped flying southward in the fall may be attributed to fewer spring migrants or to higher or less direct flight—only butterflies that are flying low and unidirectionally will strike the central barrier, rise, and work their way into the catching device of a flight trap.

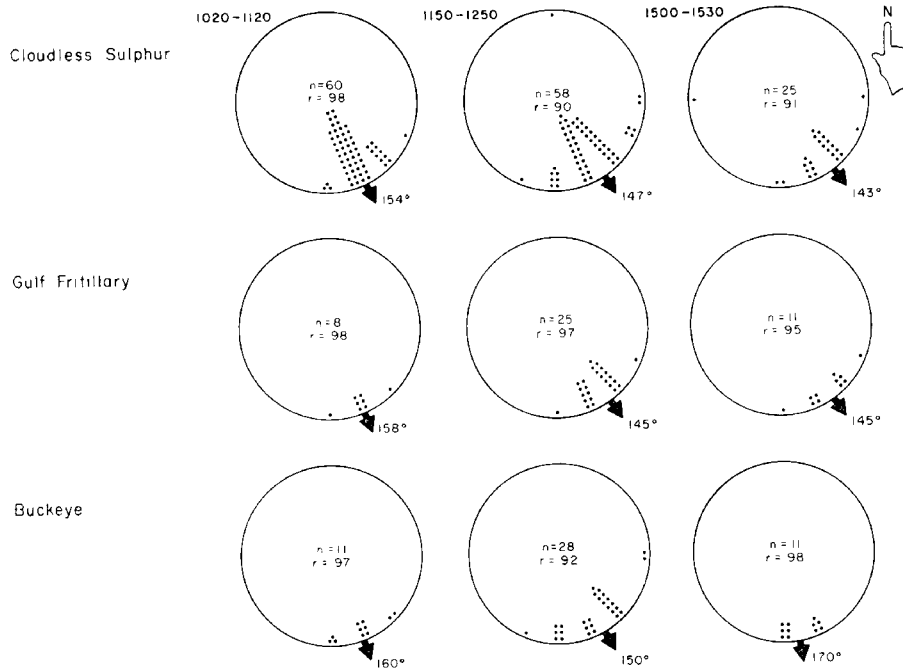


Fig. 3. Flight directions of 3 species of butterflies observed during 3 periods (times at top), 7 October 1962, Gainesville, FL. All individuals crossing a circle with a diameter of 15 m (cloudless sulphur) or 7.5 m (gulf fritillary, buckeye) were classified as to which of 16 compass directions they were flying. Arrows show mean vectors; r is a measure of scatter about mean vector (Batschelet 1965).

RETURN FLIGHTS IN MOTHS

Visual monitoring of migratory flights of moths is seldom possible—most moths fly at night and are difficult to identify on the wing even when flying in daylight. Monitoring with Malaise traps seems a likely alternative, except that most migratory flights of moths are apparently above the boundary layer and out of reach of conventional flight traps.⁹

The migratory movements easiest to demonstrate for moths are flights that result in seasonal reoccupation of areas from which earlier populations have disappeared (e.g. northward movements of species in Table 1). In a few species return trips can be substantiated with the same logic—the moth occupies only 1 area at 1 time of year and only another at another; therefore, to-and-fro migration must occur. The best documented examples are for the bogong moth of eastern Australia¹⁰ and the army cutworm of western United States (Fig. 6). Both are noctuids, as are the 5 moths in Table 1, and each flies to aestivation sites in the mountains in the spring and then to breeding sites on the plains in the fall. Directional flights in appropriate directions have been reported for both species (Common 1954, Pepper 1932, Pruess and Pruess 1971), though the importance of such observations has been questioned (Johnson 1969: 453).

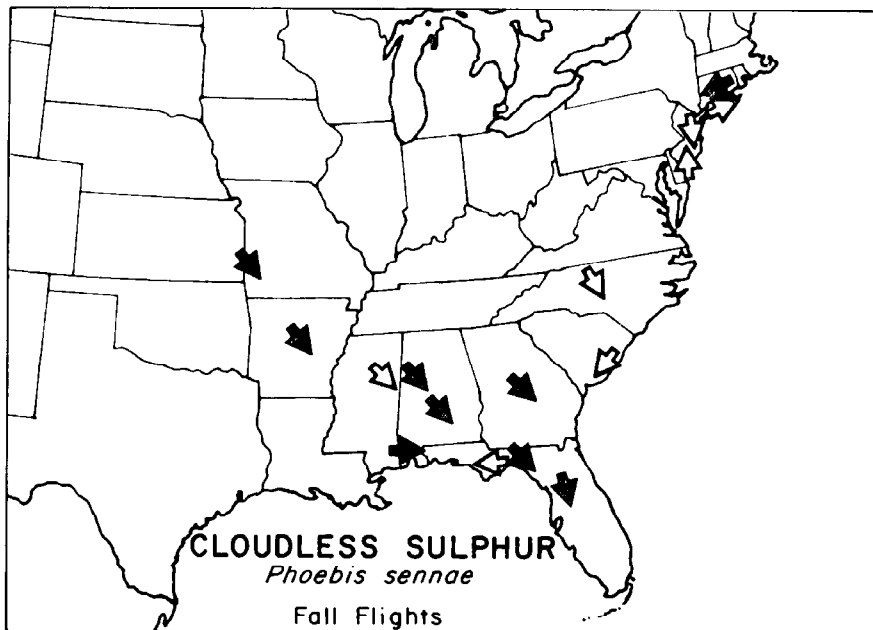


Fig. 4. Observed directions of late summer and fall migratory flights of cloudless sulphur (data from Williams 1930, 1958; Lambremont 1968; Howe 1975; Urquhart and Urquhart 1976; Muller 1977; personal observations). Solid arrows are observations made during more than 1 year.

At any rate, noctuid moths can migrate in opposite directions at appropriate seasons, and individuals of the 5 species in Table 1 would benefit by migrating southward in the fall from summer breeding areas in the North. Without visual observations or flight-trap counts, how can the occurrence, or nonoccurrence, of return flights by the 5 be demonstrated? The hypothesis of return migration warrants certain predictions that are subject to refutation by experiment. The 4 tests that seem strongest are discussed below in order of increasing cost.

Behavior in tethered flight. The flight of a tethered insect can indicate whether it would migrate if free, and if so, what heading it would take. For example, Dingle (1978) used duration of tethered flight in milkweed bugs (*Oncopeltus fasciatus*) as an index of migration potential and showed that long flights were more frequent when bugs had been reared under fall-like conditions of lower temperatures (23 vs 27 C) and shorter photoperiods (12L:12D vs 16L:8D). Sothibandhu and Baker (1979) used a specially constructed flight monitor to record the orientation of moths flying tethered in the field; the moths showed compass orientation (without time compensation) so long as the moon or stars were visible.

For the 5 species of moths in Table 1, long-duration tethered flights should be characteristic of moths reared under photoperiods and temperatures typical of the North in late summer and fall and, especially if the moths are reared at high densities, of the South in spring. Furthermore, orientation should be southward for the former and northward for the latter.

Flights to "wrong" places. The hypothesis of return flights implies that

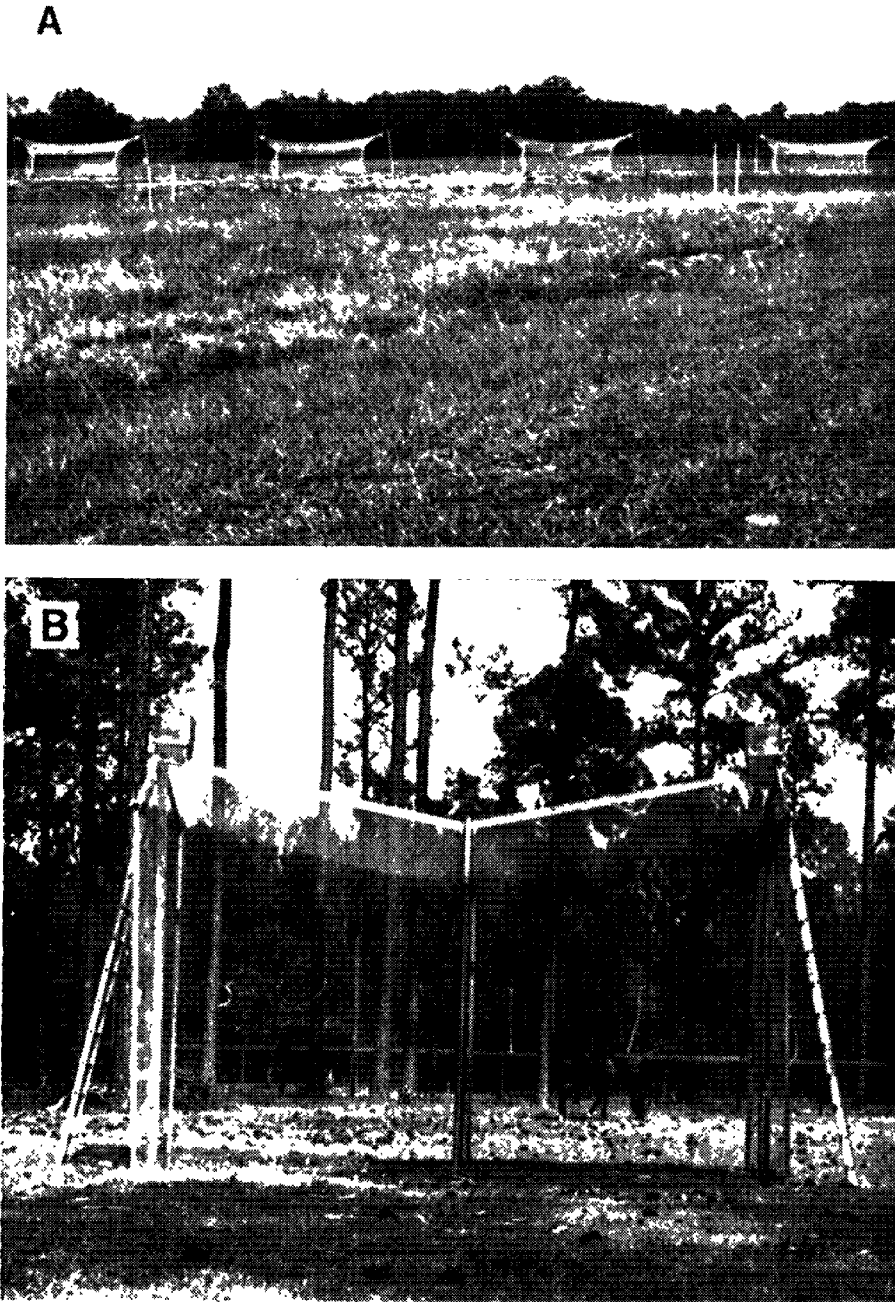


Fig. 5. Two-way flight traps used for monitoring migration in the boundary layer, Gainesville, FL. (a) Four polyester net traps used fall 1978 (Walker and Riorden 1980). Openings are ca. 6x2 m. (b) Hardware cloth (1.3x1.3-cm mesh) malaise trap used 20 March 1979-date. Opening to either side is ca. 6x3 m. Catching devices at either end are covered with 6x6-mm mesh hardware cloth.

TABLE 4. FALL MIGRATION OF BUTTERFLIES THROUGH GAINESVILLE, FL, AS REVEALED BY 2-WAY FLIGHT TRAPS.
N = intercepted flying northward; S = intercepted flying southward.

Species	Numbers collected						Estimated net number flying southward/km (1000's) ^{††}		
	"1975"*		1978**		1979†		"1975"	1978#	1979
	N	S	N	S	N	S			
Cloudless sulphur	10	244	62	1195	20	174	184	240 ± 56	128
Buckeye	17	178	27	122	1	3	104	13 ± 3	1
Gulf fritillary	0	93	7	396	1	23	42	53 ± 25	12
Bean leafroller	38	2453	51	1008	—	—	3956	406 ± 148	—
<i>Urbanus dorantes</i>	15	46	0	0	—	—	41	—	—
<i>Panoquina ocola</i>	1	164	7	97	—	—	210	38 ± 24	—
<i>Lerema accius</i>	9	54	9	26	—	—	74	7 ± 6	—
<i>Eurema lisa</i>	2	17	1	37	5	19	33	15 ± 11	23

*Data from Walker (1978). Linear Malaise traps of polyester netting with central barriers oriented WSW-ENE (perpendicular to the axis of the Florida peninsula); 1 or 2 operated 18 Sept.-26 Nov. 1975, 26 Aug.-17 Sept. 1976.

**Four traps like those in 1975-76 operated 29 Aug.-12 Nov. 1978 (Walker and Riorden 1980).

†One linear Malaise trap of 1.25x1.25 cm mesh hardware cloth (Fig. 5b), 26 Aug.-26 Nov. 1979, central barrier oriented WSW-ENE. Individuals of species other than the first 3 could easily pass through the hardware cloth mesh, but those of *Eurema lisa* apparently did not.

††Estimated number moving southward across a 1-km WSW-ENE line in excess of those moving northward. Trapping efficiency estimated at 10% except for *P. senecae* (20%), *P. coenia* (30%), and *A. vanillae* (30%).

#Mean (n=4) estimate ± 95% confidence interval.

TABLE 5. SPRING MIGRATION OF 4 SPECIES OF BUTTERFLIES THROUGH GAINESVILLE, FL, AS REVEALED BY 2-WAY FLIGHT TRAPS.

	Numbers collected						Estimated net number flying northward/km (1000's) ††		
	1976*		1978**		1979†		1976	1978	1979
	N	S	N	S	N	S			
Cloudless sulphur	2	0	3	1	0	0	—	—	—
Buckeye	155	45	126	16	191	7	50	35	102
Gulf fritillary	11	2	2	0	1	0	3	—	—
Bean leafroller	0	1	1	0	—	—	—	—	—

*Data from Walker (1978). One trap of polyester netting, 26 Feb.-9 Apr.; 2 traps, 10 Apr.-26 May.

**Data from Dave Doying (unpublished); 1-4 traps of polyester netting, 31 Mar.-13 May.

†One hardware cloth trap (Fig. 5b), 20 Mar.-26 May.

††Estimated number moving northward across a 1-km WSW-ENE line in excess of those moving southward. Trapping efficacy was estimated at 30%.

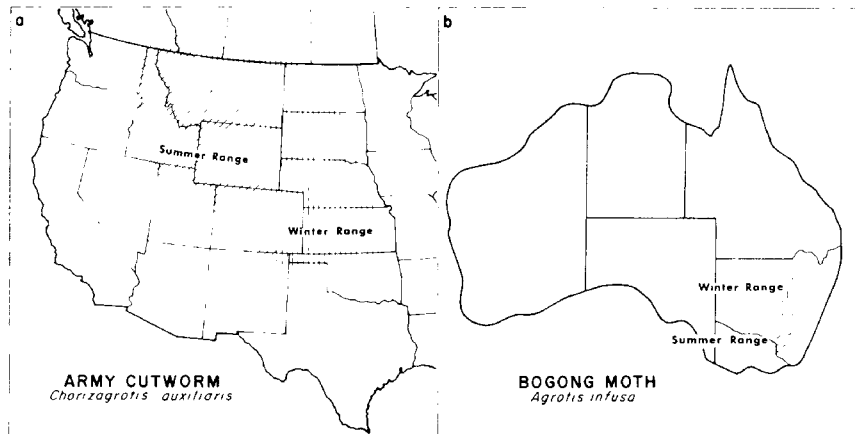


Fig. 6. Approximate summer and winter ranges of 2 noctuid moths. (a) Army cutworm spends summers in Rocky Mountains and is a pest of winter wheat in the Great Plains (Pruess 1967). (b) Bogong moth spends summers in Australian Alps and in the winter is a pest of wheat and other crops on the Western Slopes to the north (Common 1954).

the moths in Table 1 fly in such a way as to have a high probability of reaching certain areas, specifically northern breeding areas in spring and southern overwintering areas in late summer and fall. Since migratory flights apparently occur at altitudes where wind speeds exceed the moth's air speed (see below), moths must time their takeoffs to take advantage of favorable winds: they must predict in what direction the upper air will carry them. Many cues are useful for such weather prediction (Muller 1979). For example, the first warm evenings in the spring in the South usually coincide with northward winds. However, weather prognostication is uncertain, especially if local conditions are the only data that can be used. The best programmed moth may occasionally fly into the upper air and be carried in a disastrous direction. This line of reasoning leads to the following prediction: when moths end up in nonadaptive ("wrong") places, weather patterns should be anomalous. Testing this prediction calls for monitoring some of the wrong places with light traps—e.g. drilling platforms in the Gulf¹¹ and areas north of normal breeding areas. Whenever large numbers of moths are collected in a "wrong" place and back-tracked to their appropriate source,¹² the initiating weather (specifically the aspects that moths sense) should be of a type that normally correlates with upper winds flowing in an adaptive direction. For example, large numbers of fall armyworm moths (as revealed by large numbers of eggs laid) arrived at Sault Ste. Marie, Ontario, on the night of 3-4 Sept. 1973. Rose et al. (1975) concluded that they had come from northern Mississippi, 1600 km to the south, in about 30 h in association with convective storms at the source and a northward low-level jet wind.

Recapture of marked moths. Releasing marked moths may seem a hopelessly optimistic procedure for discovering where moths go, especially since moths are too small to carry informative labels such as used by Urquhart (1960) on monarchs and Roer (1968) on nymphalid butterflies. Furthermore, moths are nocturnal and marked ones are unlikely to be visually detected

and then captured. However, a group of Chinese researchers that marked and released hundreds of thousands of field-collected oriental armyworm moths (*Pseudaletia separata*) recovered at least 7 spring-marked moths >500 km to the north and 1 fall-marked moth 800 km to the south (Li et al. 1964, Baker 1978). The labor (and cost) of marking moths can be reduced by machines such as the 1 developed by Wolf and Stimmann (1972) for cabbage looper. It automatically marked up to 1500 moths an hour with colored ink without adversely affecting their longevity or mating ability. Rare elements could be added to the inks to permit detection of false positives (Southwood 1978: 78).

The most economical way to use marked moths to test for moth migration patterns in the eastern United States would combine marking and releasing massive numbers of field-collected or field-reared moths at mid latitudes (35-40°) with extensive light trapping to the north and south. Movement in early summer should be predominantly to the north; in the fall, predominantly to the south. Instances of contrary movements should be analyzed as suggested in the previous section.

Radar observations with aircraft support. Modern radar units can be used to track the flight of individual insects for several kilometers¹³ and to determine their altitude, heading, and ground speed. Unfortunately, radar images are inadequate to identify the species of insect being tracked, though by measurements of size and wingbeat frequency a mosquito or locust need not be confused with a moth (Schaefer 1976). The species followed can be inferred when masses of a single species are known to be taking off or landing in the observation area (cf. desert locusts or spruce budworm moths). Otherwise, identification must depend on aircraft collection of samples from the observed flight. The same aircraft can be used to monitor temperature and wind conditions bearing on flight behavior. Thus far, the most surprising finding from radar observations of migrating insects is that individuals in a flight at a given altitude are usually maintaining the same heading (even at night and though widely spaced). The heading is generally downwind, making the insect's ground speed 2-6 m/s faster than wind speed (Schaefer 1976). Sometimes the generally-adopted heading differs strongly from downwind. For example, Riley (1975) reported a night-time flight of insects (probably locusts) at a height of ca. 900 m in which individuals were maintaining a common northeastward heading and flying at an airspeed of 5 m/s directly into a 2 m/s southwestward wind (i.e. ground speed was 3 m/s northeastward).

Radar observation with aircraft support could be used in eastern United States to study flights of the moths listed in Table 1. The hypothesis of a return flight would be refuted if their flight behavior did not enhance their chances of traveling southward in the fall.¹⁴

DISCUSSION

In the fall, butterflies return from breeding areas at higher latitudes. Moths probably do, their migratory flights differing from those of butterflies in ways summarized in Fig. 7. The preeminent determiner of the differences seems to be that moths fly at night and butterflies in daylight. A proof of

Optimal height for migratory flights should increase from day to night for a variety of reasons. During daylight, visually hunting aerial insectivores

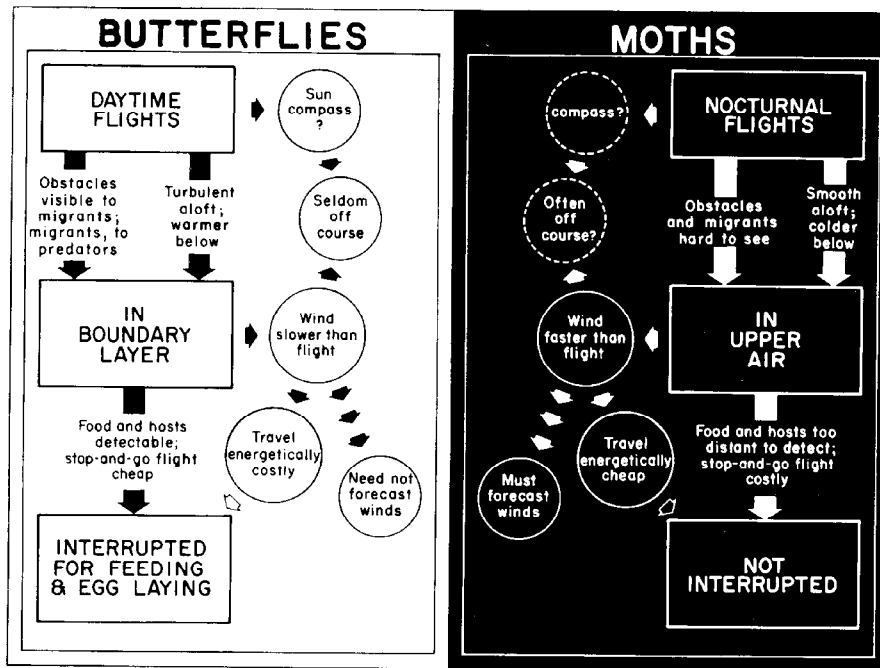


Fig. 7. Comparison of flight strategies in migrating butterflies and moths. this conjecture is that day-flying moths that migrate do so in the manner of butterflies (e.g. 2 species of the genus *Urania*, Williams 1958). The counter case, night-flying butterflies that migrate, is unknown.¹⁵

—such as kites and large swifts—make it dangerous to fly so high that refuge cannot be reached quickly.¹⁶ At night, insects flying near the ground are at greater hazard from obstacles that must be visually avoided and from spider webs. During the day the smoothest (i.e. least turbulent) and warmest air is near the ground.¹⁷ At night the smoothest and warmest air is often at the top of a thermal inversion, exactly where migrating moths sometimes fly (e.g. Johnson 1969: 449; Schaefer 1976: 188).¹⁸

Flying low permits detection of food and host plants and makes it easy for the migrating insect to stop briefly and feed or lay eggs. Migrating butterflies frequently feed when they come upon suitable food (Richman and Edwards 1976); in some species most migrating females have mated and carry mature eggs (Williams 1930, Walker 1978); they presumably oviposit along their migratory route.¹⁹ On the other hand, flight in the upper air does not facilitate detection of food or hosts, and stop-and-go migration would involve long descents and ascents. Since traveling in the boundary layer is both slower and energetically more costly per km than traveling downwind in the upper air, feeding during near-ground migration may be necessary as well as convenient.

Migrating in the upper air likewise has problems as well as benefits. Since the velocity of upper-air wind generally exceeds the migrant's air speed, the migrant loses options and ease of control as to its direction of travel. Unless it forecasts the winds correctly, it may travel in a direction opposite that of its heading (assuming that it is programmed to fly in a par-

ticular compass direction) and may terminate its flight farther from a suitable place than where it started. Whether moths migrating at night can maintain compass orientation as butterflies do in daylight (Fig. 3) is uncertain.²⁰ Even if they can, the speed of the wind and the difficulties in detecting wind direction make moths at greater risk of gross errors in navigation than butterflies. However, moths that reach their programmed destination may do so much more quickly than butterflies, and the average total migratory risk for moths and butterflies need not be different.

Are butterflies better at migrating than moths? Maybe, maybe not; but they surely do it differently.

ACKNOWLEDGEMENTS

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APPENDIX

¹Annual movements to breeding areas at higher latitudes occur in at least 6 insect orders: ORTHOPTERA, *Schistocerca gregaria*, Johnson 1969: 571; HEMIPTERA, *Oncopeltus fasciatus*, Dingle 1978; HOMOPTERA, leafhoppers and aphids, Johnson 1969; COLEOPTERA, *Diabrotica undecimpunctata*, Johnson 1969: 414-5; LEPIDOPTERA, this paper; DIPTERA, *Musca vetustissima*, Hughes and Nicholas 1974, Hughes 1979.

²The difficulty with negative evidence is well illustrated by R. R. Baker's (1978: 425-33) recent speculation that about 30% of *D. plexippus* in the Great Lakes region hibernate rather than migrate southward. Experimental evidence for inability to overwinter is surprisingly scanty and restricted to *A. vanillae* (Randolph 1927), *T. ni* (Elsey and Rabb 1970), and *S. frugiperda* (Wood, Poe, and Leppla 1979). More research of this type is of critical importance in refining the questions relative to migration of the species in Table 1. The weakest case for inclusion of a species in Table 1 is for *P. coenia*. I have found no definite statement as to its absence in the North in winter. Mather (1967 and personal communication) reported it overwintering as far north as Jackson, MS. Interestingly, it is the only species other than the monarch with strong evidence for a northward flight in the spring (Table 5).

³The first *D. plexippus* to arrive is much more likely to be seen than the first *S. frugiperda*. Detailed mapping, based on extensive, systematic observations, is yet to be done for any species. The best data are for *T. ni* and *P. includens* but the observations were limited to South Carolina and southward. The lack of suitable data may be illustrated by *P. coenia*. Howe (1975: 137) reported it to occur north to southern Ontario and New England, but how regularly does it reach that far north? When it does, does it successfully breed there?

⁴Unidirectional travel need not depend on a constant individual heading. If the individual flies, in any direction, in an air stream that is moving much faster than the individual's air speed, the individual's track will be chiefly in the direction of the air stream. Only if emigration occurs near the ground, where wind speeds are substantially less than air speeds, will the individual's heading be the chief determinant of its track.

⁵C. B. Williams (1958: 132) understood and stated the dilemma clearly: "If the habit of long-distance migration has persisted in certain insects for

(presumably) millions of years, and if every individual which shows the habit flies away from the breeding ground and is lost (as far as continuing the species is concerned), then we have to admit that a habit which is completely fatal to all individuals possessing it can continue to persist for countless generations!"

⁶The proposed program is more complicated, and perhaps more realistic, than the one implied in Table 2 and in the discussion of frequency-dependent selection. In Table 3, flying northward or staying in the overwintering area in the spring is made conditional on density. The same genotype can produce either behavior, and there need be no equilibrium between genotypes that have the potential for one or the other (but not both). Dawkins (1979) distinguished 3 phenomena that lead to continued mixtures of behaviors within a deme: stable polymorphism, individual mixed evolutionarily stable strategy, and conditional strategy. The strategy outlined in Table 3 for migratory Lepidoptera is conditional; a stable polymorphism was described in the discussion of maintaining a mixture of the first 2 behaviors in Table 2. Cade (1980), in this symposium, applied Dawkin's classification to male reproductive behaviors.

⁷Aphids are especially useful in demonstrating conditional genetic programs because members of parthenogenetic clones can be studied, with all differences in phenotypes attributable to different environments.

⁸The boundary layer for an insect is the layer near the ground in which its air speed exceeds wind speed, giving the insect potential control of its track. The thickness of the boundary layer varies with wind speed and with the insect's air speed. The 4 species in question generally fly within 2 m of the ground. The monarch often flies higher but is more powerful and has a top air speed of at least 40 km/hr (Urquhart 1960). It is also an accomplished soarer (Gibo and Pallett 1979).

⁹The flight traps that detected spring and fall migratory flights of butterflies at Gainesville were operated 24 h per day and caught significant numbers of moths. However, no biases in flight direction of the magnitude typical of migrating butterflies were detected (Walker 1978, C. S. Barfield, unpublished data).

¹⁰Common (1954: 256) doubts that all Bogong moths aestivate, reporting that an "occasional larva has been collected in a garden at Canberra in December." However, he gives no evidence for summer breeding in the plains to the north.

¹¹A. N. Sparks (Sparks et al. 1975 and unpublished) ran blacklight traps on unmanned oil platforms as far as 160 km from shore in the Gulf of Mexico, south of Jeanerette, LA, 9 Sept.-21 Oct. 1973. The *S. frugiperda* and *S. exigua* he collected (numbers but not dates given in Mitchell 1979) could be used to test this hypothesis—provided these moths do not normally migrate across the Gulf of Mexico to Central America in the fall.

¹²Back-tracking involves plotting the location of migrants at various preceding times and dates on the basis of data and assumptions about wind conditions, flight altitude, and flight speed. For examples, see Johnson 1969: 516-23, and Rose et al. 1975.

¹³The most commonly available radar units can track a single moth at distances no greater than 2 km, but more specialized units can stretch this to ca. 8 km. Swarms of moths can be detected at greater distances (Schaefer 1976, Skolnik 1978).

¹⁴To enhance their chances of traveling southward, moths might (1) fly upward and submit themselves to passive transport in the upper air only when local conditions were indicative of southward winds, (2) maintain southward headings and fly only when the resulting track was southward—i.e. fly only if winds are southward or too light to prevent progress southward. Merely flying upward and maintaining altitude does not qualify as "return

flight" (*sensu* Fig. 1), even if it sometimes has the same result. As Rainey (1978) pointed out, wheat rust fungi, by means of airborne spores, occupy northern summer breeding areas each spring and return southward in the fall. In making a "return flight," a moth must exert better control over its destination than does a fungus spore.

¹⁵Williams (1930: 341) cited numerous records of migratory butterflies flying at night, but most relate to individuals that may have been over water since dusk.

¹⁶"The remarkable exception" (Williams 1930: 338) to migrating butterflies flying within a few meters of the ground is the monarch (see also Gibo and Pallett 1979). However, monarchs are protected to a large extent from bird predation by a heavy load of cardenolides acquired during larval feeding (Brower and Glazier 1975). Nocturnal flights above the boundary layer are endangered by predators too: echo-locating bats can catch flying insects in total darkness. However, noctuid moths have tympana that are sensitive to the hunting sounds of bats and can sometimes take successful evasive action (Roeder 1966).

¹⁷Within the daytime *convective layer*, the region of thermally induced mixing that sometimes extends upward 1 km or more, turbulence increases with altitude at least for the first 50 m or so (Kaimal et al. 1976). The warmth of the boundary layer air may be of importance to butterflies because they require a thoracic temperature of at least 27 C for controlled flight (Douglas 1979) yet have a slow wingstroke rate and are not as well insulated as moths.

¹⁸Turbulence increases above the inversion layer. The fact that temperatures are less above and below the top of the inversion layer is of uncertain significance. Moths are insulated by their scales and can fly in cold air, but whenever they are unable to maintain optimal flying temperature using only the heat generated as a byproduct of flight, they can increase their efficiency by flying in warmer air.

¹⁹No data exist on the frequency of oviposition by butterflies enroute to overwintering areas. Laying eggs has value only if the resulting progeny have time to complete their development and follow their mother equatorward. Since a generation requires ca. 1 month (Urquhart 1960, Arbogast 1965) and fall migration lasts up to 2 months (Walker 1978, Walker and Riorden 1980), early migrants should benefit from laying eggs. Arbogast (1965: 30-3) found a peak of egg laying by *A. vanillae* corresponding to the first half of fall migration through Gainesville, FL. Butterflies flying poleward in the spring should oviposit because they are entering unexploited yet suitable habitats and suitability of habitats farther along, and their own survival, are uncertain.

²⁰The means of orientation in migrating butterflies has not been proved, but field observations (Fig. 3) are compatible with their using a time-compensated sun compass, or a magnetic compass (Arbogast 1965, Kanz 1977, Lindauer 1977). Nocturnally migrating moths cannot use a sun compass, yet they can maintain a common heading (Schaefer 1976). That this heading is generally downwind suggests that the orientation may be in relation to the air stream rather than to the points of the compass. However, orienting to an air stream while in it, especially at heights and times that make visual cues from the ground unlikely, is at least as hard to explain as heading in a compass direction at night. Actually, selecting an airstream that is moving in the migratory direction may require that the moth do both!

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