BIOLOGY AND MIGRATORY BEHAVIOR OF *AGRAULIS VANILLAE* (L.) (LEPIDOPTERA, NYMPHALIDAE)

By

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

Figure Page

INTRODUCTION

Migration has been defined by Schneider (1962) as a prolonged escape movement in which there is a tendency to maintain a constant direction and which results in the permanent or periodical abandonment of a habitat. Migration can be classified as dispersive, contractive, or collective according to the spatial effect. Many insects migrate in this sense, and numerous accounts of their migrations can be found in the literature. Recent reviews of insect migration have been published by Schneider (1962) and Williams (1957, 1958).

In most of the migratory insects which have been carefully studied, the migratory direction is determined largely by the prevailing wind. Swarms of the desert locust (*Schistocerca gregaria* Forsk.) are carried downwind, and since the winds in the lower few thousand feet of the atmosphere may be regarded ultimately as blowing from areas of high pressure to areas of low pressure, the downwind displacement results in movement into areas of low pressure where abundant rainfall produces conditions favorable for the reproduction of the locust (Rainey, 1951). The migratory direction of the coccinellid *Hippodamia convergens* Guérin-Méneville in California is determined by the prevailing winds at its flight level (Hagen, 1962). In the summer, the prevailing winds at this level are from the low lands toward the mountains where aggregation occurs, and in the winter, they are from the mountains to the low lands. The mosquito *Aedes taeniorhynchus* Wiedemann migrates downwind (Provost, 1952, 1957).

In contrast to this, many migrating butterflies maintain, over long distances, a constant direction which is influenced little by wind, topography, or time of day (Williams, 1958). The determination of migratory direction appears to be under the control of the insect itself, but the nature of the underlying orientation mechanism has remained obscure. Only two migratory butterflies have been studied in great detail (Nielsen and Nielsen, 1950; Nielsen, 1961; Urquhart, 1960), and these studies did not include an investigation of the orientation mechanism. Recent work on the orientation of other animals has suggested new approaches to this problem. (For references, see Long Island Biological Association, 1960.) The purpose of the research reported here, was to study the migratory behavior of the gulf fritillary, *Agraulis vanillae* (L.), against the background of its general biology and to investigate the nature of the orientation mechanism involved in maintaining the migratory direction.

The gulf fritillary is a member of the essentially neotropical nymphalid subfamily Heliconiiae. Michener (1942) recognizes eight subspecies as follows:

> *Agraulis vanillae vanillae* (Linnaeus) occurs in northern South America, Panama, and the southernmost of the Lesser Antilles.

Agraulis vanillae insularis Maynard ranges throughout the Bahamas and the Antilles except for the southernmost Lesser Antilles.

Agraulis vanillae maculosa (Stichel) is found in northern Argentina, Paraguay, southern Brazil, and Chile.

Agraulis vanillae forbesi Michener occurs in the coastal region of Peru.

Agraulis vanillae galapagensis Holland is restricted to the Galapagos Islands.

Agraulis vanillae lucinia C. and R. Felder occurs on the eastern side of the Andes in Ecuador, Peru, and Brazil.

Agraulis vanillae incarnata (Riley) is occasionally found as far north as British Columbia but more commonly occurs in southwestern United States, Mexico, and Central America.

Agraulis vanillae nigrior Michener is the subspecies of southeastern United States but is occasionally found as far north as New York.

The migratory habit has evolved in at least two of these subspecies. Definite migrations of A. v. nigrior to the north in the spring and to the south in the fall have been observed in Florida (Williams, 1958). Hayward (1962) reported an eastward migration of A. v. maculosa at Tucamán, Argentina, on January 7, 1961. The research reported here was restricted to A. v. nigrior. This form intergrades with A. v. incarnata in Texas and thence southward but is distinct from A. v. insularis.

The early stages of _A_. _v_. _nigrior_ were described long ago (Edwards, 1880; Scudder, 1889), but no detailed studies of its biology have been made. More recently, detailed descriptions of the early stages of _A_. _v_. _vanillae_ have been published (Beebe, Crane, and Fleming, 1960) and certain details of the adult morphology have been described by Emsley (1963). The biology and behavior of the larvae, pupae, and emerging adults of _A_. _v_. _vanillae_ were discussed by Alexander (1961a, 1961b) and compared with those of other members of the subfamily occurring in Trinidad.

LIFE HISTORY

Methods and Materials

Rate of development

Rearing to determine the rate of development was initiated with eggs obtained from females which had mated in cages. These cages were 14 inches square and 24 inches high with sides of aluminum screen and top and botton of ¼ inch plywood. A 9 inch square opening in the top covered with a plate of glass served as a door. One or more males and one or more females which had been reared in captivity from larvae were confined in a cage and placed outdoors in direct sunshine. Mating was obtained in this manner using males 1-3 days after emergence and females 0-3 days after emergence. Mating occurred in both the morning and the afternoon and usually within 2 hours after the butterflies were placed in the cage. Occasionally no mating occurred even when the butterflies were left in the cage all day, but frequently the same butterflies would mate when placed in the cage the next day.

One to 3 days after mating, the females were confined individually with cuttings of Passiflora incarnata L. This was accomplished either by introducing a jar of water containing the cuttings into the mating cage or by placing a cheesecloth bag over cuttings contained in a flower pot full of damp sand

and then confining the butterfly in the bag. The latter method was the most satisfactory. The confined butterflies deposited many eggs on the side of the cage or on the cheesecloth bag. It was difficult to remove the eggs from the side of the cage without damaging them, but those deposited on the cheesecloth could be removed by cutting out the piece of material to which they were attached.

The captive butterflies were fed once a day on sugar water of variable concentration. A cotton ball was saturated with the solution and placed in a small dish containing additional solution. The butterfly to be fed was grasped by the wings and its tarsi touched to the cotton ball. Usually this caused the butterfly to extend its proboscis and begin feeding. Butterflies which refused to feed when touched to the cotton ball could often be induced to feed by uncoiling the proboscis and inserting its tip in the sugar water. Once feeding began, the butterflies remained quietly on the cotton ball until feeding was completed.

The time required to complete each stage of development at each of two constant temperatures was determined by rearing the insects in a constant temperature cabinet. In one case, the temperature in the cabinet was maintained at 23-24° C. and in the other case at 28.5-29.5° C. To determine the time required for the eggs to hatch, 1-7 hour old eggs were placed in the cabinet in a covered petri dish and checked once a day for hatching. To determine the duration of the remaining stages, the insects were reared individually from egg to adult in pint fruit jars.

The caterpillars were kept supplied with one or two leaves of the food plant. Each individual was examined once a day and the dates of hatching, molting, pupation, and emergence were recorded.

The larvae suspended for pupation from the lids of the jars or from the point just below the neck where the sides curve inward. In both cases the point of attachment was too smooth and many of the chrysalides fell. This difficulty was overcome by placing a piece of coarse-textured paper (toweling) beneath the lid and inserting a screen cylinder which extended from the bottom to the top of the jar. The larvae crawled up the cylinder and suspended successfully from the paper.

Longevity of the adults

In order to gain some idea of the adult life span, butterflies which had been reared from eggs in pint fruit jars at a temperature of 23-24° C. were confined individually in cubic screen cages 4 inches on a side and left in the constant temperature cabinet at the same temperature. They were fed daily as described above.

Reproductive development of the female

The elapsed time between the emergence of a female and the maturation of the eggs in the ovaries was determined. For this purpose, larvae in various stages of development obtained from the field and from eggs laid by females in captivity were reared together on food plant cuttings in screen cages in a greenhouse. The larvae were crowded but were kept abundantly supplied with food, and the adults which were produced were of normal size. When the adults began to emerge, it became apparent that all emergences occurred during the morning, so the cages were checked each day at 1 hour intervals between 0600 and 1200 Eastern Standard Time. Each time, all the butterflies that had emerged during the preceding hour were removed and the time of emergence recorded as the time midway between the last two checks. Thus the time of emergence recorded for each individual was accurate within ± 30 minutes. The females were confined in pint fruit jars with screen lids and left in the greenhouse for periods of 0-48 hours with 6 hour increments. They were then preserved by injecting them with 10 per cent formalin and placing them in 3 per cent formalin. The preserved butterflies were dissected and the ovaries examined.

Behavior of adults and larvae

The behavior of larvae of all stages and of adults was observed in the field and in screen cages. In order to observe the manner in which periods of larval feeding alternate with periods of rest and walking, fifth instars were brought into the laboratory from the field, and each was placed on a bunch of food plant cuttings in a screen cage. The larvae were observed for 4 hours, and the times at which feeding began and ended were recorded for each individual. These observations were made in the afternoon of a cloudy day, and the cages were located in front of a southwest window. The sun occasionally shown through the clouds, and as a result, the light intensity in the cages varied considerably. However, there was no correlation between feeding activity and the light intensity.

The Egg and Oviposition

The larvae feed upon Passiflora incarnata and probably other plants of the genus, and the females oviposit upon and in the vicinity of these plants. Ovipositing females fly low over and through the vegetation, frequently pausing to hover about individual plants. When the butterfly contacts the larval food plant, it alights and deposits an egg. Actual contact with the plant seems to be essential for the release of oviposition. Mated females confined with food plant cuttings deposited an egg only after actually touching the cuttings. Mated females confined without cuttings did not oviposit. The stimulus which releases the act of oviposition is probably provided by a chemical which is characteristic of this genus of plants and which is detected by gustatory organs in the tarsi or antennae of the butterfly.

The position of the egg depends upon where the female is able to gain a foothold after contacting the food plant. Most eggs are deposited upon the upper surfaces of the leaves, but some are deposited on the undersurfaces, stems, tendrils, buds, and nearby objects. The butterfly curves the abdomen ventrad until the oviducal pore contacts the object upon which it has alighted, whereupon it deposits an egg. In this process, the tip of the abdomen may be turned through more than 270 degrees. A female which lands on a leaf surface near the margin of the leaf often curves the abdomen around the margin and deposits an egg on the opposite surface. It was noted previously that females confined in cages with food plant cuttings deposit many of their eggs on the side of the cage. This results from the fact that the butterflies frequently land on the side of the cage after fluttering about and coming in contact with the cuttings. Ovipositing females were observed on a small planting of _P. incarnata_ along the side of a building. Frequently they would strike the side of the building and alight after coming in contact with the plants. Each time this occurred, they deposited an egg on the side of the building.

Observations of females in the field and in cages indicate that there is always a period of flight after the deposition of each egg. Several eggs were often found on the same leaf, but this was probably the result of several visits. In some cases, this was borne out by the fact that some of the eggs were yellow, while others were reddish brown (see following paragraph). This behavior distributes the eggs more evenly over the available food supply. Furthermore, larvae in captivity were observed chewing into unhatched eggs, even in the presence of abundant food. The spacing of the eggs brought about by the egg laying behavior of the female reduces losses of this sort.

The eggs are yellow when deposited, but become reddish brown within 24 hours. Thirty-nine eggs kept at a temperature of 23-24° C. hatched on the fifth day. Thirteen eggs kept at a temperature of 28.5-29.5° C. hatched on the third day.

The Larva

The larva is illustrated in Figures 1 and 2.

Figure 1. Fourth instars of *Agraulis vanillae nigrior* Michener.

Figure 2. Fifth instar of *Agraulis vanillae nigrior* Michener.

Upon hatching, the young larva consumes the eggshell before beginning to feed upon the food plant, and newly hatched larvae were frequently observed eating unhatched eggs which they happened to encounter, even in the presence of abundant food. The caterpillars feed mainly upon the leaves, but when food becomes scarce, they feed upon the exterior portions of the buds and fruit and strip the epidermis and cortex from the stems. The first three instars generally feed away from the leaf margins. Newly hatched larvae feeding upon thick tough leaves eat only the epidermal cells of one surface and the mesophyll cells, leaving the epidermis of the opposite surface intact. Newly hatched larvae feeding upon thin tender leaves and older larvae in general cut holes completely through the leaves. The two final instars feed at the leaf margins. When ample food is available, the portion of a leaf which is eaten before it is abandoned varies considerably. The petioles are almost always left but may be eaten, at least in part, when food becomes scarce. Larvae were never observed eating one another, even when kept in crowded cages without food. In two instances, however, larvae kept under these conditions were observed eating chrysalides.

Alexander (1961a) studied the feeding rhythms of 10 species of heliconiine butterflies in Trinidad, including *Agraulis vanillae vanillae* (L.) and found that feeding periods of about 20-30 minutes alternate with rest periods of similar duration. Four fifth instars of *Agraulis vanillae nigrior* Michener observed feeding in the laboratory showed a similar feeding rhythm. Feeding periods of about 10-60 minutes alternated with periods of rest and walking of about 10-90 minutes (Figure 3).

Frequently a larva cuts a girdle 2-3 mm. wide around a stem. This girdle extends only through the epidermis and cortex and does not kill the plant. Larvae were observed cutting these girdles many times in the field and in cages, and large numbers of plants were found with healed wounds of this kind. In one case which was timed, girdling of the stem required 10 minutes (Figure 3D). Alexander (1961a) found similar behavior in the larvae of several heliconiine butterflies but apparently not in the larvae of _A. v. vanillae_. The caterpillars of _Heliconius melpomene_ (L.) and _H. ricini_ (L.) chew furrows across the midribs of leaves, while the caterpillars of _Dryas julia_ (Fabr.) and _Dryadula phaetusa_ (L.) cut narrow channels from the margins to the midribs. In all cases this behavior is exhibited during a rest period and it is therefore unlikely that the material is eaten solely for its nutritive value. Alexander suggested that the furrowing and channeling behavior might be a form of territory marking. Perhaps the girdling behavior of _A. v. nigrior_ also represents territory marking, but no evidence was obtained to either prove or disprove this hypothesis.

The rate of development of the larva varies with temperature (Figure 4). The mean duration of the larval stage was 15.7 days at 23-24° C. and 11.5 days at 28.5-29.5° C. These means are significantly different at the 1 per cent level.

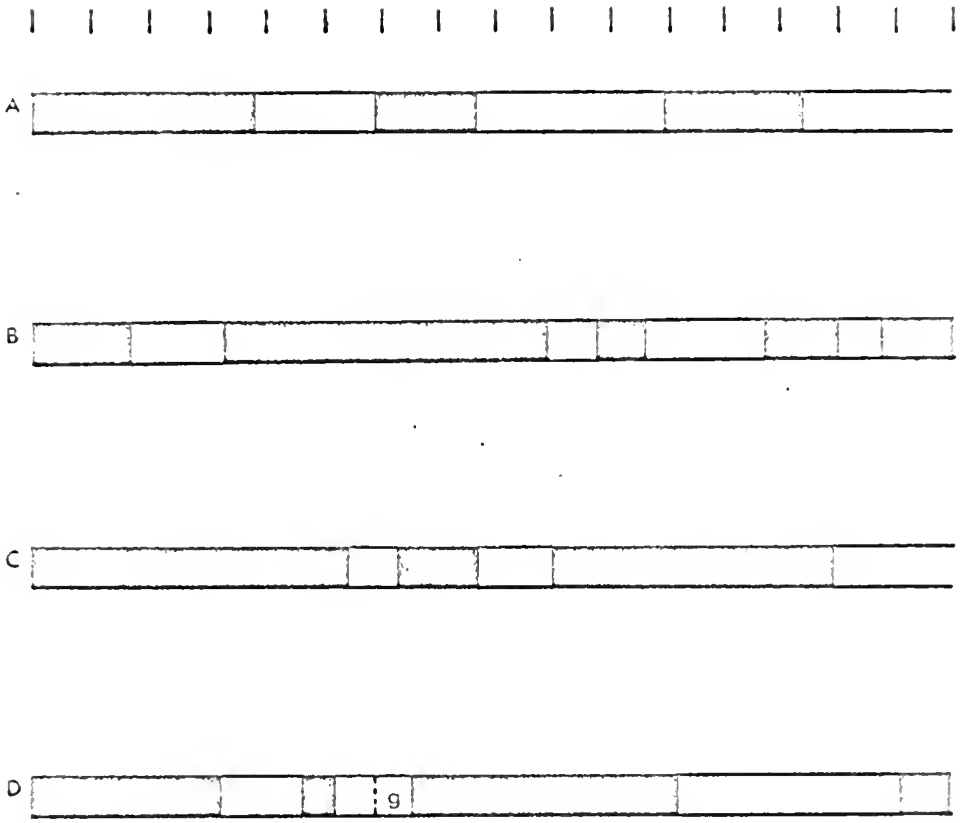


Figure 3. Feeding rhythms of fifth instars. Black represents resting and walking, white feeding, and g girdling. Each division at the top is 15 minutes.

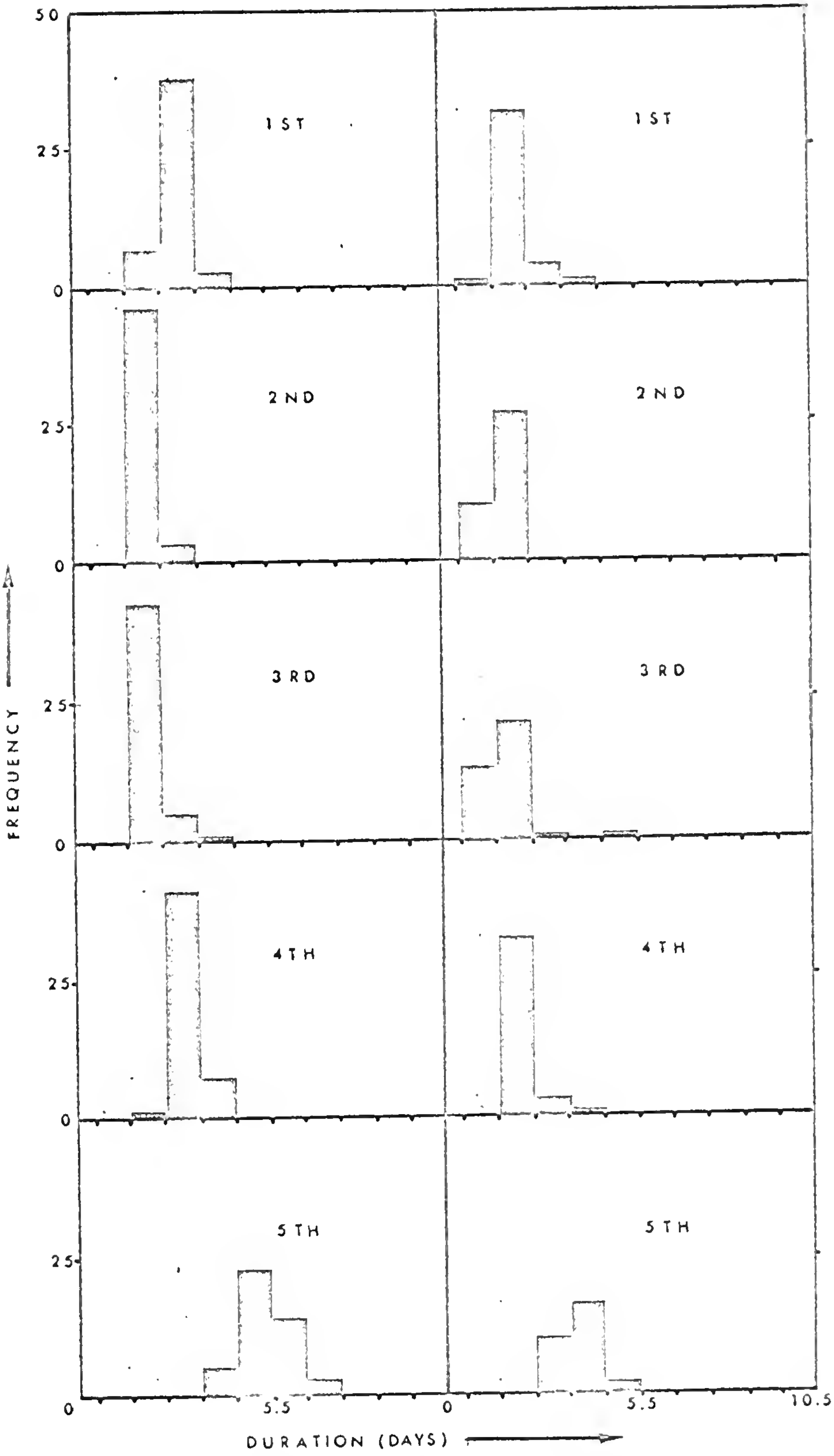


Figure 4. Duration of the various instars at 23-24° C. (left) and at 28.5-29.5° C. (right).

The molting and pupation behavior of *A. v. vanillae* was described in detail by Alexander (1961b). This probably does not differ in most respects from that of *A. v. nigrior*. However, Alexander reported that *A. v. vanillae* almost invariably pupates on the stem, tendrils, flowers, or leaves of its food plant. *A. v. nigrior* usually pupates on objects at some distance from the food plant.

The Pupa

The pupa is illustrated in Figures 5 and 6.

Histograms of the duration of this stage are presented in Figures 7 and 8. The mean duration was 11.7 days at 23-24° C. and 7.5 days at 28.5-29.5° C. These means are significantly different at the 1 per cent level.

The Adult

Emergence

Apparently most emergence from the chrysalid occurs during the morning. Butterflies which were reared from larvae in a greenhouse during September under the natural day-night cycle emerged between 0600 and 1200 with maximum emergence occurring between 0900 and 1000 (Figure 9). On the days during which emergence occurred, morning civil twilight began at approximately 0550 and sunrise was at approximately 0610. Alexander (1961b) noted a similar time of emergence for the heliconiine butterflies *Heliconius erato* (L.) and *H. melpomene* in Trinidad.

Upon emergence, the butterfly hangs from the pupal skin

Figure 5. Dorsal view of pupa of <u>Agraulis vanillae nigrior</u> Michener.

Figure 6. Lateral view of pupa of Agraulis vanillae nigrior Michener.

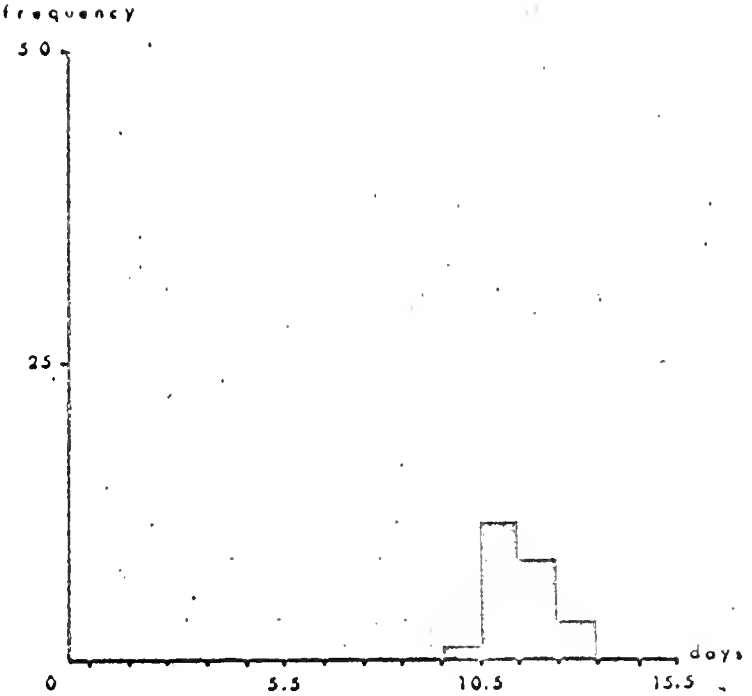


Figure 7. Duration of pupa at 23-24° C.

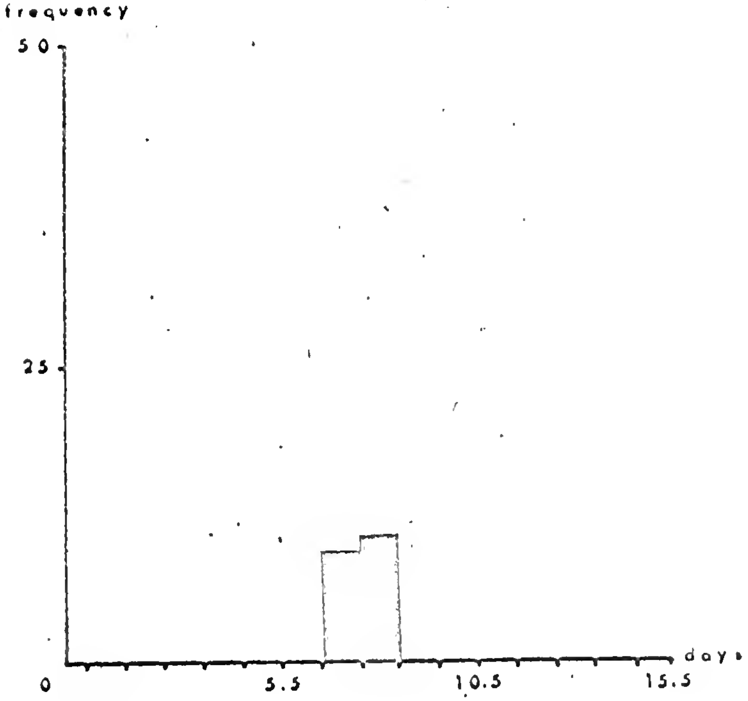


Figure 8. Duration of pupa at 28.5-29.5° C.

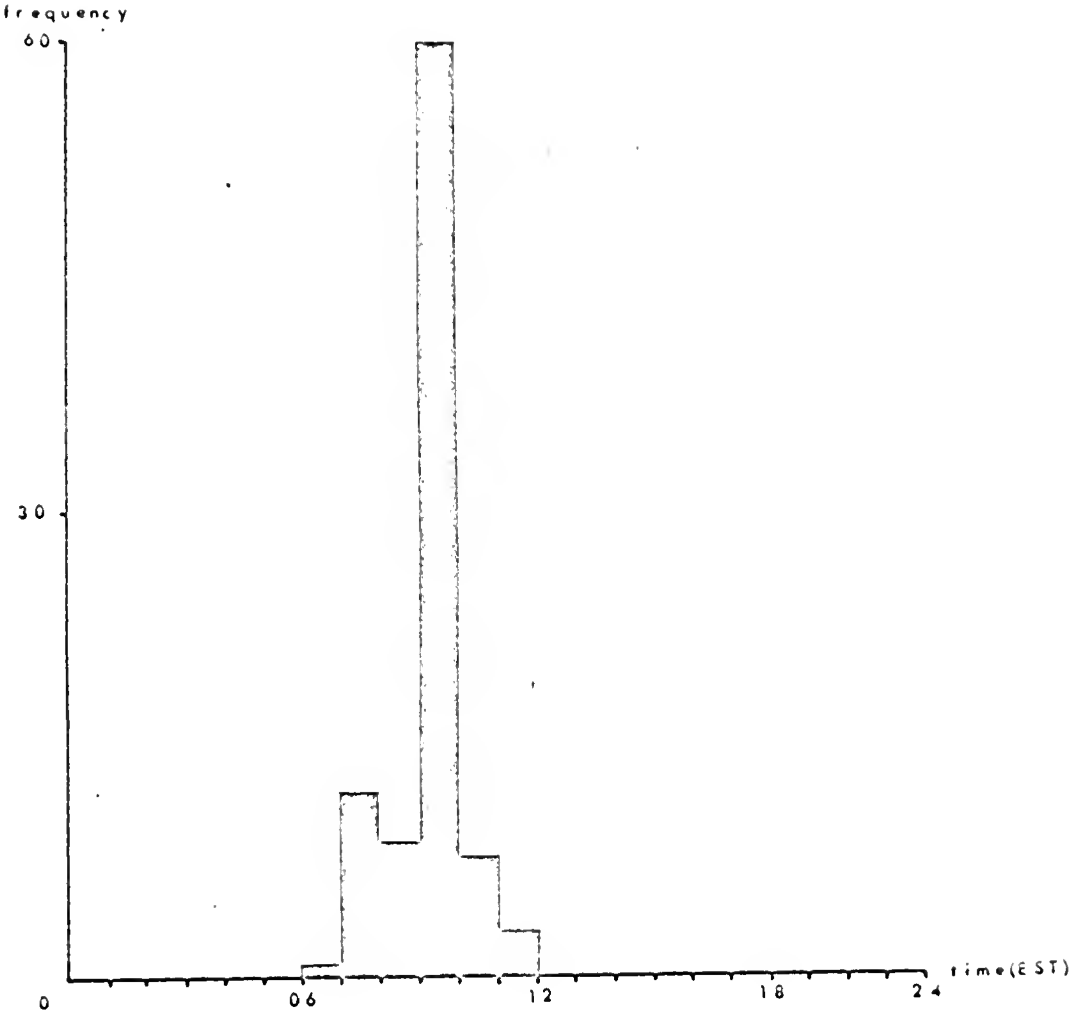


Figure 9. Time of emergence of the adult.

until the wings have expanded and dried (Figure 10). Expansion of the wings requires from 3-4 minutes, and they are dry enough for flight within an hour.

Sex ratio

Of 265 butterflies which emerged in captivity 54 per cent were males and 46 per cent females. This sex ratio is not significantly different from 1:1 at the 5 per cent level.

Reproductive development of the female

Dissections of preserved females indicated that most individuals reach reproductive maturity 12-18 hours after emergence, although a few individuals are still not mature 48 hours after emergence. Mature eggs could be recognized in the preserved specimens by their morphology. In these eggs, there was a central dark yellow mass occupying no more than 3/4 the volume of the egg, and the transparent chorion was very conspicuous. In the immature eggs, the entire volume of the egg was occupied by cream colored or pale yellow material, and the chorion, when it was present, was not so conspicuous. Length proved to be an unreliable criterion for determining egg maturity. Oviposited eggs which subsequently produced larvae ranged in length from 1.30-1.60 mm. All the mature eggs fell within this size range. However, in several cases immature eggs 1.30 mm. long were found.

Mating behavior

Females will mate within 24 hours after emergence and will mate at least as long as 3 days after emergence as pointed out in the discussion of methods and materials. Males will

Figure 10. Recently emerged adult of *Agraulis vanillae nigrior* Michener hanging from the pupal skin.

mate at least as early as 1 day after emergence and as late as 3 days after emergence. No experiments were conducted to determine the two extremes of age at which each sex will mate.

No courtship was observed in the field, and that observed in cages was probably greatly abbreviated. The confined butterflies alternately rested on the sides of the cage and fluttered against the sides and top of the cage. When a fluttering male approached a resting female, the female usually responded by elevating the abdomen and vibrating the wings with the hind wings opened 90 degrees and the fore wings opened about 45 degrees. Then the male would land beside the female facing the same direction, vibrate his wings, and thrust at the female's abdomen with the end of his abdomen. During this process, the female would continue to vibrate her wings in the described position. When the ends of the abdomens came in contact, the male would grasp the end of the female's abdomen with his claspers and then turn 180 degrees to assume the copulatory position. Occasionally mating occurred even when the female showed no response to the male. When both the male and the female were fluttering, the female would land on the side of the cage, and the process would proceed as described. Copulation lasted from 45-60 minutes. A detailed study of the mating behavior including the roles played by motion, color, size, shape, pattern, and odor remains to be done. Crane (1955) has made such a study of the related butterfly *Heliconius erato*, and many of her conclusions will probably be found to apply equally well to *Agraulis vanillae*.

Longevity of the adults

Nine males and nine females kept in a constant temperature cabinet at 23-24^{o} C. lived from 14-27 days after emergence. The mean life span was 18.4 days with a standard deviation of 3.0 days. There was no significant difference between the mean longevity of the males and females at the 10 per cent level. Since these butterflies were unmated and were not subjected to the same stresses normally encountered in nature, the observed life span is perhaps slightly longer than that of the species in nature.

DISTRIBUTION OF LARVAL FOOD PLANTS

Presumably any species of *Passiflora* can serve as a food plant for *Agraulis vanillae nigrior*, but only *P. incarnata* was examined for eggs and larvae. Only two species of *Passiflora* are widely distributed in the United States (Killip, 1938). *Passiflora incarnata* ranges from Virginia to Missouri and south to Florida and Texas but has been introduced farther north. *Passiflora lutea* L. ranges from Pennsylvania to Illinois and Kansas and southward to Florida and Texas.

Seven species of *Passiflora* have been recorded from Florida (Killip, 1938), but no detailed account of their distribution within the state has been published. A general idea of their distribution was obtained from specimens in the herbarium of the University of Florida Agricultural Experiment Station. Apparently *P. sexflora* Juss., *P. pallens* Poepp. ex Mast., *P. multiflora L.*, and *P. foetida* L. are restricted to the extreme southern portion of the state. *Passiflora lutea* occurs in northern penninsular Florida and in West Florida. *Passiflora suberosa* L. ranges throughout peninsular Florida. *Passiflora incarnata* occurs throughout the state but is apparently less common in the south and west. With the exception of *P. incarnata*, which occurs largely in old fields and along roadsides, these plants appear to occur largely in wooded areas.

POPULATIONS OF *Agraulis vanillae* IN THE VICINITY OF GAINESVILLE, FLORIDA

Description of Observed Breeding Areas

Adult gulf fritillaries can be found in almost any open situation. However, at least in north central Florida, their reproduction is limited to rather small widely scattered areas by the patchy nature of the food plant distribution. Four such areas in the vicinity of Gainesville, Florida, with growths of *Passiflora incarnata* were selected for observation (Figure 11). Area 1 measured approximately 120 x 220 feet and lay in an old field with growths of broomsedge (*Andropogon glomeratus* /Walt./ BSP) and Blackberry (*Rubus* sp.). Late in the summer the food plants were almost hidden by a dense growth of ragweed (*Ambrosia artemisiifolia* L.). Area 2 measured approximately 50 x 70 feet and was also in an old field with growths of broomsedge and blackberry, but ragweed was absent. Area 3 measured approximately 90 x 200 feet. The dominant plants were broomsedge, blackberry, groundsel-tree (*Baccharis halimifolia* L.), elder (*Sambucus canadensis* L.), and shining sumac (*Rhus copallinum* L.). The growth of *Passiflora* in this area was extremely dense. Area 4 measured approximately 90 x 140 feet and lay in a pine flatwoods. Longleaf pine (*Pinus palustris* Mill.) was the dominant plant. There were widely scattered shrubs including

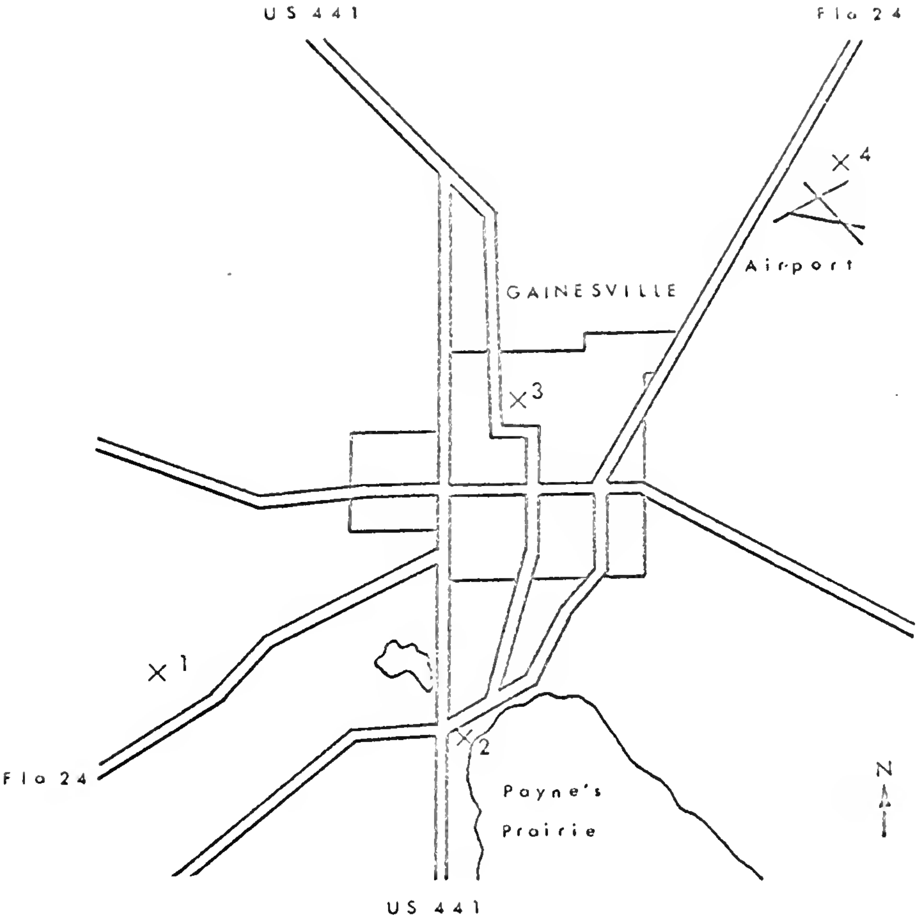


Figure 11. Breeding areas in the vicinity of Gainesville, Florida

waxmyrtle (Myrica cerifera L.), live oak (Quercus virginiana Mill.), water oak (Quercus nigra L.), Daubentonia punicea (Cav.) DC, groundsel-tree, and shining sumac. Blackberry was a dominant plant of the ground cover.

Fluctuations in the Observed Populations

It was not possible to obtain an estimate of the actual number of eggs and larvae present in a given breeding area at a given time. However, it was possible to obtain an index of this number and thereby observe fluctuations. This was done by arbitrarily choosing 75 plants in such a way that all portions of the breeding area were represented and counting the number of eggs and larvae on the terminals and first six leaves. Later in the season, when the plant population began to decline, it was sometimes not possible to find 75 plants. In this case, as many plants as could be found were examined.

The number of plants examined and the number of eggs and larvae found at various times between July, 1964, and May, 1965, are presented for each of the four observed breeding areas in Tables 1-4. In all cases except Area 4, the number of eggs and larvae increased slightly during July and then remained fairly constant until the end of August when there was a rapid increase. Area 4 was apparently unoccupied until the latter part of August when large numbers of eggs and larvae appeared there. In all cases this rapid increase in numbers caused a marked reduction in the available food. The available food was reduced further in Area 1 by large numbers of blister beetles

TABLE 1

OBSERVED NUMBER OF EGGS AND LARVAE IN AREA 1 (1964-65)

Date	Plants	Eggs	Larval Instar					Eggs and Larvae
			1	2	3	4	5	
1 Jul	75	0	0	1	0	0	1	2
22 Jul	75	17	0	0	0	0	3	20
28 Jul	75	10	1	0	1	1	0	13
5 Aug	75	25	3	0	0	0	3	31
15 Aug	75	15	0	0	1	0	1	17
27 Aug	75	62	22	3	2	2	7	98
6 Sep	75	51	19	6	3	14	7	100
29 Sep	75	17	21	14	2	18	14	86
20 Oct	42	3	16	6	3	11	12	51
12 Nov	11	0	0	1	11	2	2	16
2 Dec	5	0	0	0	0	1	1	2
20 Dec	3	0	0	0	0	0	0	0
14 Mar	0	0	0	0	0	0	0	0
3 Apr	75	0	0	0	0	0	0	0
15 Apr	75	0	0	0	0	0	0	0
2 May	75	0	0	0	2	1	2	5

TABLE 2

OBSERVED NUMBER OF EGGS AND LARVAE IN AREA 2 (1964-65).

Date	Plants	Eggs	Larval Instar 1	2	3	4	5	Eggs and Larvae
8 Jul	75	0	0	0	0	1	0	1
16 Jul	75	0	0	0	0	0	2	2
22 Jul	75	1	0	2	3	3	3	12
4 Aug	75	5	2	6	3	7	10	33
12 Aug	75	5	0	0	1	3	9	18
19 Aug	75	17	1	0	2	3	1	24
26 Aug	75	33	8	2	0	2	1	46
6 Sep	75	36	13	7	0	4	15	75
24 Sep	25	13	16	12	6	1	9	57
7 Oct	5	3	2	1	0	2	1	9
2 Nov	13	3	1	2	0	2	0	8
18 Nov	10	10	29	5	3	3	5	55
2 Dec	13	0	2	2	4	8	0	16
20 Dec	4	0	0	0	0	0	0	0
14 Mar	0	0	0	0	0	0	0	0
3 Apr	24	0	0	0	0	0	0	0
24 Apr	75	0	0	0	0	0	1	1

TABLE 3

OBSERVED NUMBER OF EGGS AND LARVAE IN AREA 3 (1964-65)

Date	Plants	Eggs	Larval Instar					Eggs and Larvae
			1	2	3	4	5	
18 Jul	75	0	0	0	0	1	0	1
26 Jul	75	0	0	0	0	0	1	1
4 Aug	75	3	0	0	0	1	4	8
11 Aug	75	7	0	0	2	0	1	10
18 Aug	75	8	0	0	0	1	3	12
30 Aug	75	12	1	1	4	11	11	40
20 Sep	75	44	5	0	4	5	5	63
7 Oct	75	15	15	10	9	12	26	87
20 Oct	75	10	10	2	1	3	2	28
2 Nov	75	10	7	1	1	3	3	25
19 Nov	75	12	7	4	5	7	4	39
7 Dec	75	2	2	5	3	1	1	14
28 Dec	75	4	1	0	1	3	0	9
16 Jan	75	10	6	2	0	0	1	19
4 Feb	0	0	0	0	0	0	0	0
14 Mar	13	0	0	0	0	0	0	0
3 Apr	75	1	0	0	0	0	0	1
24 Apr	75	1	0	0	0	0	2	3

TABLE 4

OBSERVED NUMBER OF EGGS AND LARVAE IN AREA 4 (1964-65)

Date	Plants	Eggs	Larval Instar					Eggs and Larvae
			1	2	3	4	5	
3 Jul	75	0	0	0	0	0	0	0
18 Jul	75	0	0	0	0	0	0	0
27 Jul	75	0	0	0	0	0	0	0
6 Aug	75	0	0	0	0	0	0	0
24 Aug	75	32	1	1	1	1	3	39
2 Sep	75	7	7	8	15	16	14	67
24 Sep	0	0	0	0	0	0	0	0
14 Mar	4	0	0	0	0	0	0	0
3 Apr	75	0	0	0	0	0	0	0
2 May	75	0	0	1	3	0	0	4

(Meloidae) which seemed to be particularly attracted to *Passiflora*. In Area 3, where the growth of *Passiflora* was very dense, the food supply remained abundant in spite of the reduction, and the destroyed plants were soon replaced by new growth. In the other areas there was only a small amount of new growth, and it soon became impossible to find 75 plants. The reduction in food plants was especially marked in Area 4 where it was impossible to find any plants 31 days after eggs and larvae were first discovered there. The insect was therefore absent from this site until the following spring. In the other localities, the number of eggs and larvae began declining in October. Area 2 showed a second peak in mid-November and then declined again. On December 1, a minimum temperature of 30° F. was recorded at Gainesville Municipal Airport (U.S. Weather Bureau, 1964). This temperature was taken in an instrument shelter 5 feet above the ground, and it is reasonable to expect that the temperature in the open near the ground was slightly lower due to the loss of heat by radiation. The terminals and young leaves of exposed plants in areas 1 and 3 were damaged by this low temperature, while those growing under shrubs were not. No damage occurred to the plants in area 2, probably due to the moderating influence of the nearby water (Figure 11). The larvae were apparently not injured by this frost. No further freezing temperatures occurred until January when minimum temperatures below 32° F. were recorded at the airport on 8 days and below 28° F. on 3 days (U.S. Weather Bureau, 1965). This was sufficiently low to kill all the plants. New shoots emerged in March. Apparently the first eggs were deposited early in April.

These observations indicate considerable overlapping of the generations. This is to be expected since the oviposition period for each female is relatively long, and the time required for the insect to pass from egg to adult is relatively short.

There were seldom more than a few adults present in a breeding area when observations were made regardless of time of day and size of larval population. Apparently the adults spend only brief periods in the breeding areas for oviposition and possibly for mating.

THE FALL MIGRATION

Methods and Materials

Observational setup

Migrations of the gulf fritillary were observed during October, 1963, and September, October, and November, 1964, in a large open field near Gainesville, Florida. A circle 50 feet in diameter was laid out in this field. The circle was marked by bottles 5 inches high and 1.5 inches in diameter buried up to their necks at 20 degree intervals around the circumference. Before each observation period, a stake 4 feet long was inserted in each of the bottles. The stakes were labeled with large black numbers beginning with 1 at north and continuing clockwise to 18. After each observation period, the stakes were removed and the bottles capped. The circle is shown set up for observations in Figure 12. Observations were made from stations 8 feet outside the circle. There was one station directly outside each stake, and they were used in random order with a different station for each day of observations.

Weather observations

Wind speed and direction were measured by means of a cup anemometer and wind vane connected to remote wind speed and direction indicators (Nassau Windmaster, Model No. 409, Science Associates, Princeton, New Jersey, Figures 13-14). The anemom-

Figure 12. Setup for observing migrations.

Figure 13. Wind vane and anemometer used in migration studies.

Figure 14. Wind speed and direction dials used in migration studies.

eter and wind vane were mounted at a height of 5 feet on a tripod placed 25 feet outside the circle and 20 degrees clockwise from the observation station (Figure 15). The remote indicators were at the observation position. Wind observations were made every half hour in 1963 and every 5 minutes in 1964. Sky cover and weather conditions were recorded every hour unless a major change occurred during the course of an hour. Sky cover was classified according to the fraction of the celestial dome covered by clouds as follows:

Clear -- less than 1/10
Scattered -- 1/10-5/10
Broken -- 6/10-9/10
Overcast -- more than 9/10

The term thin was applied to any of the above when the sun was clearly visible through the clouds. Hourly temperatures were obtained from U.S. Weather Bureau records for Gainesville Municipal Airport which is approximately 7 miles from the observation site. The temperatures were taken in a standard instrument shelter at a height of 5 feet and were probably representative of air temperatures over the entire Gainesville area.

Speed and direction of flight

In describing the flight speed and direction of migrating butterflies, it is convenient to employ the terminology of aircraft navigation. The following terms are used:

Track -- the migrant's direction relative to the ground.
Ground speed -- the migrant's speed relative to the ground.

Figure 15. Wind vane and anemometer mounted on tripod for observations.

Course -- the direction in which the migrant is heading.

Air speed -- the migrant's speed relative to the air.

Wind direction -- the direction from which the wind blows.

Wind speed -- speed of the wind.

The track of each migrant crossing the circle was determined by recording the numbers of the stakes between which it entered and left the circle. It was assumed that the points of entrance and exit were midway between the stakes through which the migrant passed. A line through the center of the circle parallel to the line through these two points gives the track within ± 10 degrees. Ground speed was determined by measuring with a stop watch the time required for a migrant to cross the circle and noting the points of entrance and exit as described above. The wind speed and direction read at the time the migrant left the circle were assumed to represent the wind speed and direction as it was crossing the circle. The ground speed, g, in miles per hour is given by the expression

$$g = 34.1 \frac{\sin \frac{1}{2}\alpha}{t}$$

where t is the time in seconds required for the migrant to cross the circle and α is the angle subtending the chord of the circle which represents the path of the butterfly through the circle.

In calculating air speed and course, angles were measured counter-clockwise from 0 to 180 degrees and clockwise from 0 to -180 degrees with respect to the vector representing the track, using the tail of the vector as the origin (Figure 16). The air speed, v, is given in miles per hour by

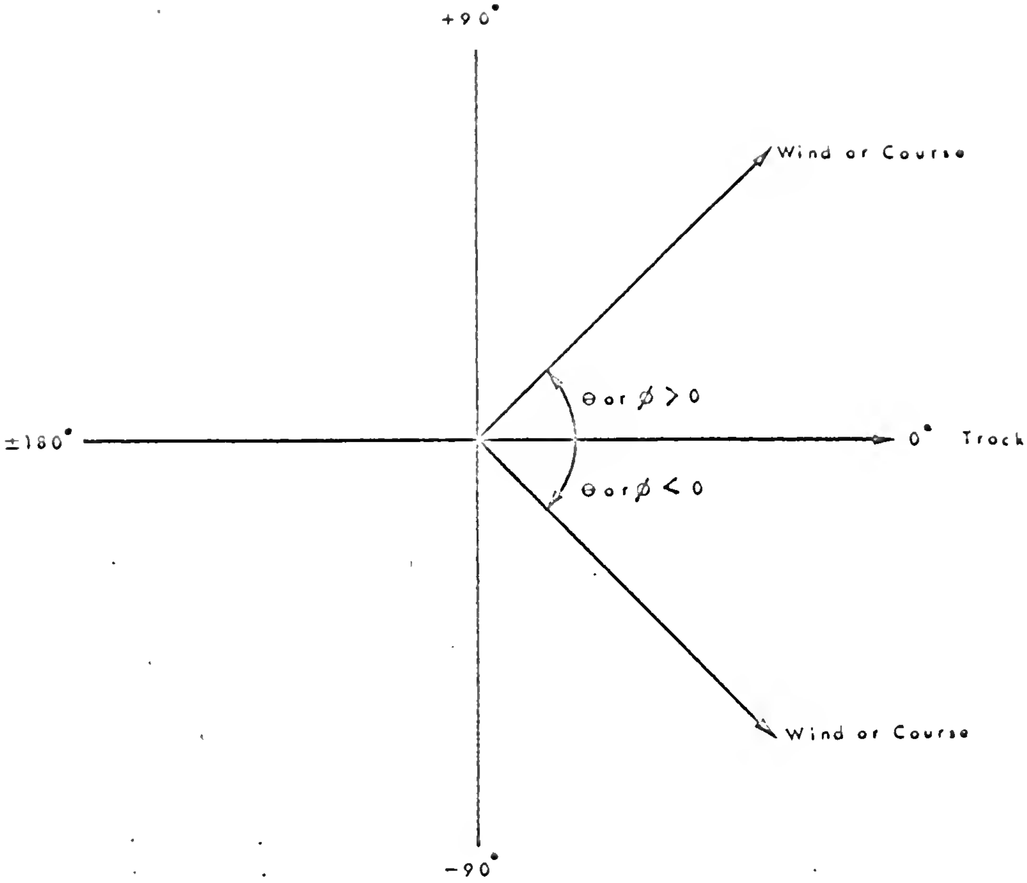


Figure 16. Convention used in measuring angles between track and wind direction (θ) and between track and course (∅).

the expression

$$v = g - w \cos \theta,$$

where w is the wind speed in miles per hour and θ is the angle between the wind direction and the track. The true bearing of the course, c, is given by the expression

$$c = a - \emptyset,$$

where a is the true bearing of the track, $\emptyset$ is the angle between the course and the track, and

$$\sin \emptyset = - \frac{w \sin \theta}{v}.$$

Density of the migration

The density of the migration is expressed as the number of migrants per mile per hour crossing a northeast to southwest line through Gainesville, Florida. This quantity was estimated by determining the number of migrants crossing the circle in one hour. Since the point of entrance or exit was inadvertently missed for some of the butterflies, this estimate was not as accurate as it might have been. Of those migrants whose track was determined, 97.8 per cent had track bearings between 100 and 180 degrees. It is apparent from the geometry of the circle that any migrant crossing the circle and having a track bearing within this range must cross a northeast to southwest line 66.4 feet long with its midpoint at the center of the circle (assuming that all migrants enter and leave the circle at points midway between two stakes). Since some of the migrants had track bearings outside this range, the assumption that all migrants passing through the circle cross this line results in a positive error in the density estimate. On the other hand, this line extends 8.2 feet beyond the circle on either side. Therefore, the assumption that only those migrants passing through the circle cross the line results in a negative error in the density estimate. Since both of these errors are probably small, and since one at least partially cancels the other, a fair estimate of the migration density can be obtained by multiplying the number of migrants crossing the circle in one hour by 79.5 (the number of times 66.4 feet is contained in 1 mile).

A better estimate could have been obtained if the points of entrance and exit had been noted for every butterfly crossing the circle. Then it would have been possible in making the estimate to consider only those migrants which crossed the northeast to southwest diameter of the circle, and both types of error would have been eliminated. Furthermore, in discussing migration density, it would be desirable to separate those butterflies which are flying southward from those which are flying northward. This could be done if the track of every migrant crossing the circle were known.

Reproductive maturity of the females and sex ratio

Migrating gulf fritillaries were captured with a butterfly net to determine the sex ratio among them. Some of the females were preserved as described previously and later dissected to determine their reproductive maturity and if they had mated.

Description of the Migration

Characteristics of the migratory flight

Migrating gulf fritillaries fly at a height of 3-6 feet over open terrain, and upon encountering an obstacle, such as a building or a wooded area, they fly up and over it without changing their direction. In general, the flight is very persistent, but occasionally they pause briefly to feed at flowers. The direction of most individuals lies between 110 and 160 degrees (Figure 17) and does not vary with time of day (Figure 18). While the path of a migrant over the earth may be influenced by the wind, the migratory direction is not determined by this factor (Figure 19). Instead, it appears to be under the control of the insect itself.

The direction of a flying animal relative to the earth's surface is determined by its motion through the air and by the motion of the air itself. If the animal maintains a constant course, fluctuations in the crosswind will cause fluctuations in its track. To maintain a constant track, it must alter its course to compensate for these fluctuations or, in other words, correct for wind drift. The crosswinds observed during this study were too light to determine if migrating gulf fritillaries make this correction.

The ground speed of a flying animal is a function of the energy it expends per unit time and of the wind component along its course. If the animal expends a constant amount of energy, its ground speed will be less with a head wind than with

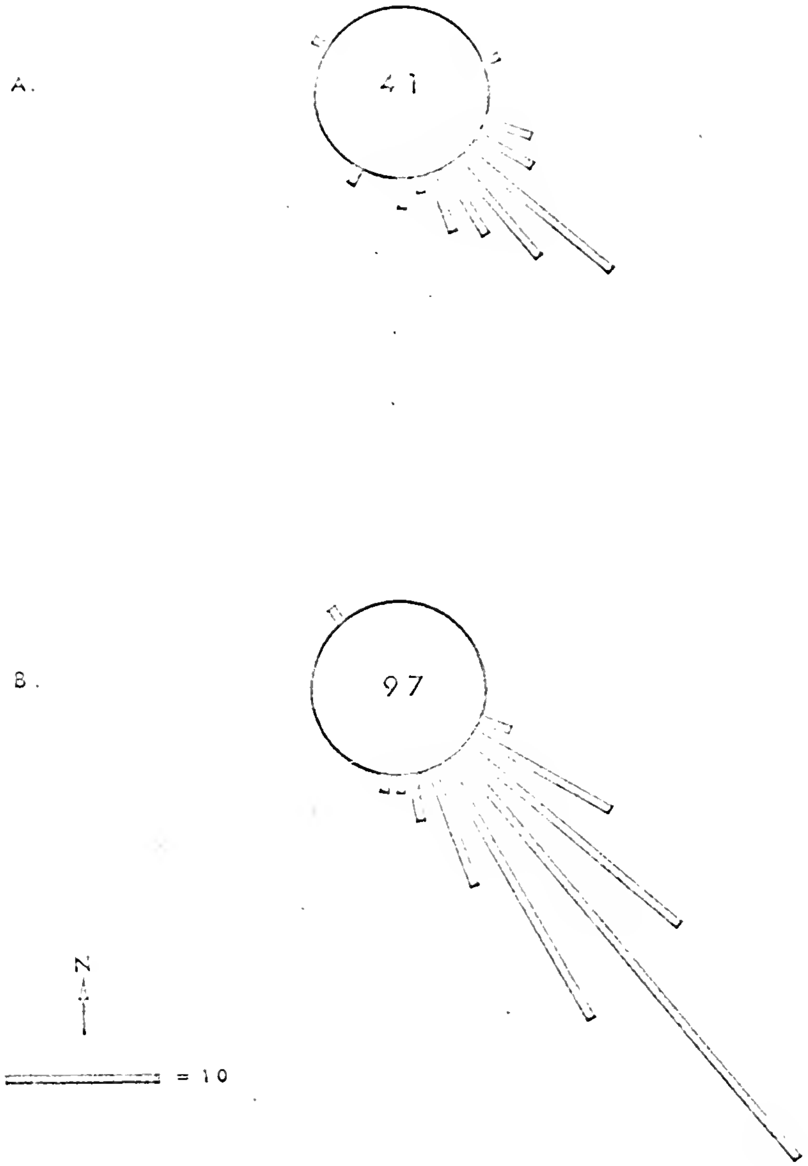


Figure 17. Tracks of migrants observed during the fall of 1963 (A) and 1964 (B). The numbers in the circles represent the total number of migrants observed in each case.

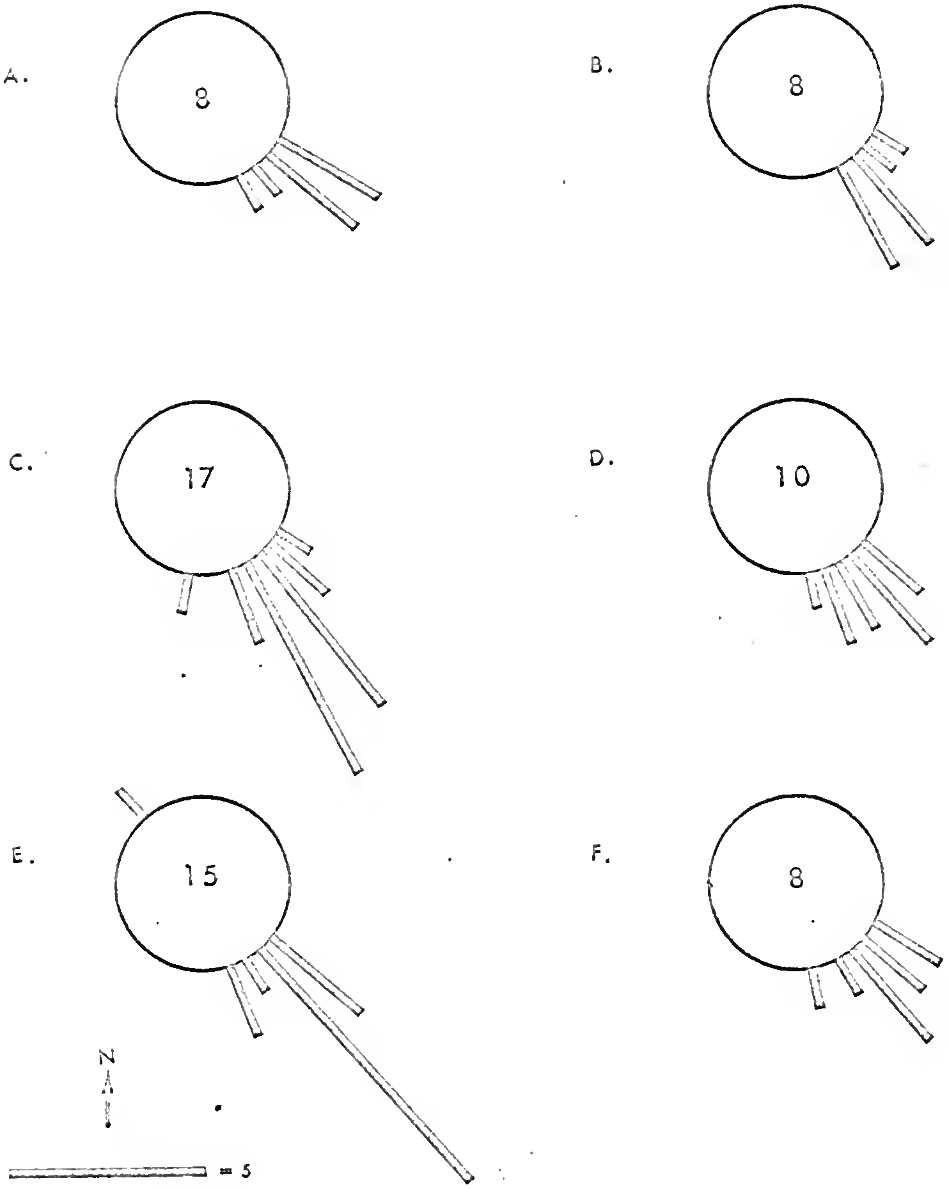


Figure 18. Tracks of migrants observed at various times of day on September 23, 1964. (A) 0800-0900 EST, (B) 1000-1100 EST, (C) 1200-1300 EST, (D) 1300-1400 EST, (E) 1400-1500 EST, (F) 1600-1700 EST. The numbers in the circles represent the total number of migrants observed in each case.

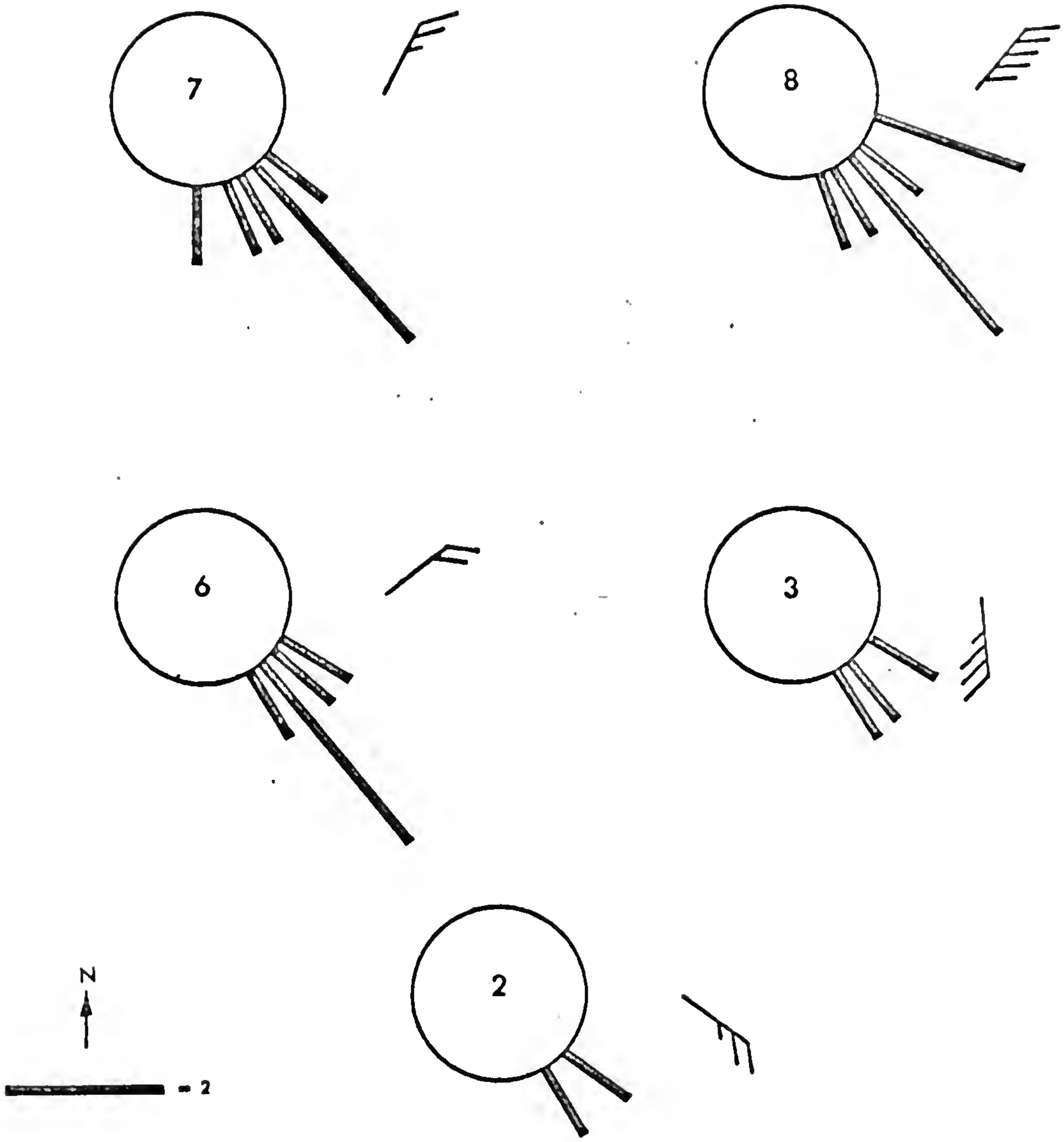


Figure 19. Tracks of migrants and mean wind speed and direction observed between 1300 and 1400 EST on various days in the fall of 1964. Wind direction is indicated in each case by the direction of the arrow. Each full barb in the tail represents 2 miles per hour of wind speed. The numbers in the circles represent the total number of migrants observed in each case.

a tail wind, while its air speed will be the same in both cases. To maintain a constant ground speed, it must alter its energy output to allow for the effect of wind, and since it is a function of the energy expenditure, the air speed will vary.

Within the range of observed winds, it appears that each gulf fritillary expends a more or less constant amount of energy, but this amount varies from individual to individual. The ground speed of 23 individuals flying in calm air ranged from 6.9-14.6 miles per hour with a mean of 10.4 (Figure 20), while that of 11 individuals flying against a head wind of 1-5 miles per hour ranged from 6.7-11.4 with a mean of 8.4 (Figure 21A), and that of 9 individuals flying with a tail wind of 1-4 miles per hour ranged from 8.8-15.6 with a mean of 12.1 (Figure 21B). The means are significantly different at the 5 per cent level. The air speed of the headwind group ranged from 8.6-14.6 with a mean of 11.2 (Figure 22A), and that of the tailwind group ranged from 8.8-13.3 with a mean of 11.0 (Figure 22B). The means are not significantly different at the 20 per cent level. It follows that the ground speed will decrease as the head wind increases until the butterfly must increase its energy output, land, or be carried backwards. Which of these alternatives actually occurs was not determined. The head winds did not reach this magnitude during the course of the present study, and they seldom do at the flight level of the migrants.

Variations in migration density

The migration densities determined between 1300 and 1400 Eastern Standard Time on various dates during the course

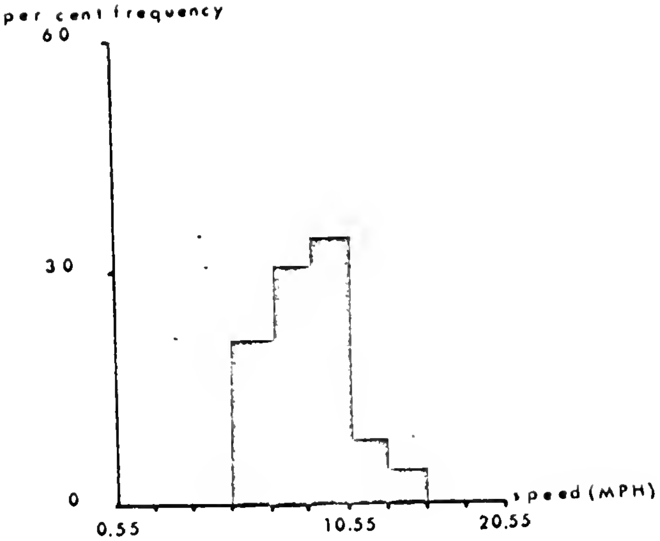


Figure 20. Ground speed of migrants flying in calm air.

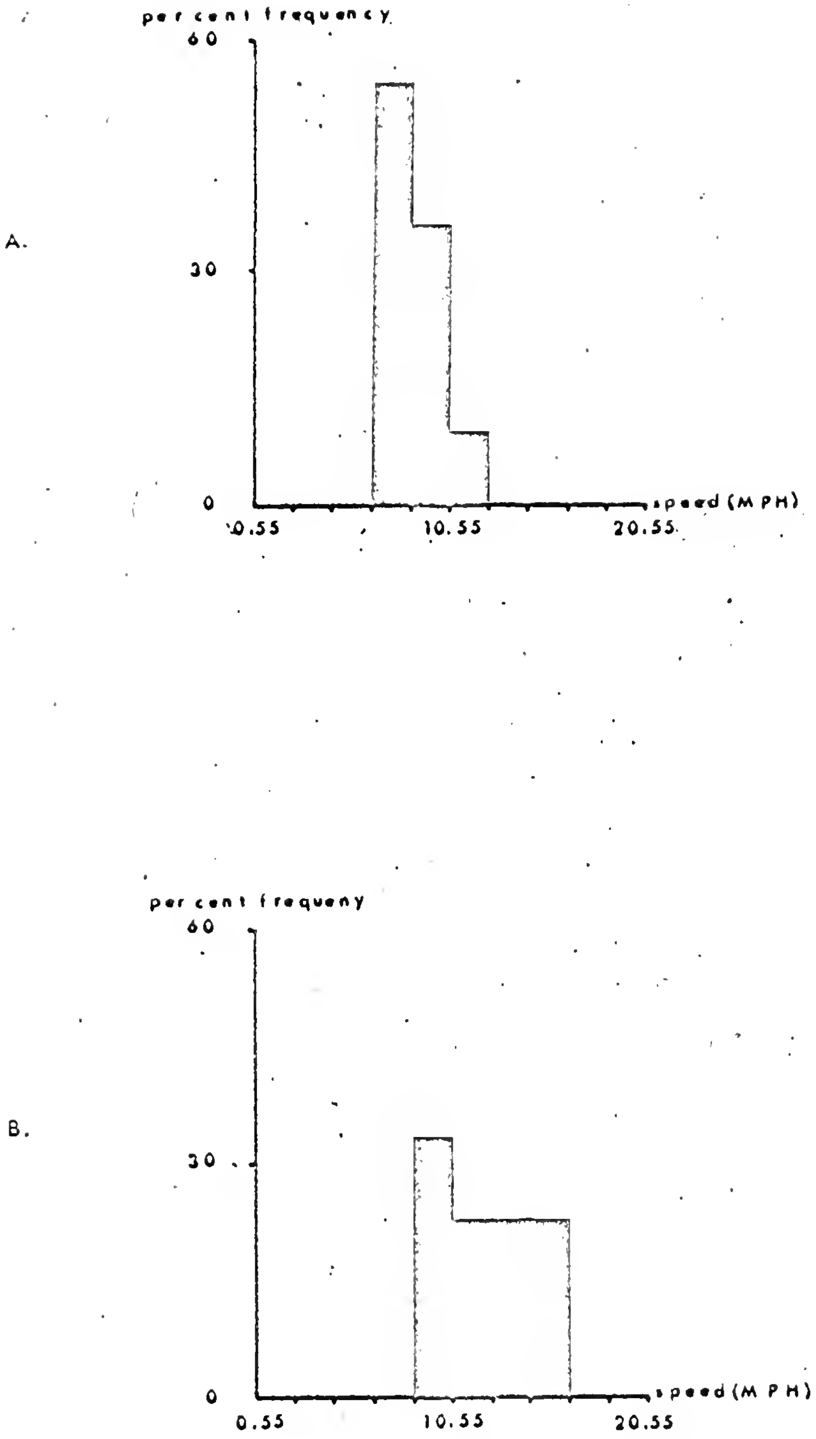
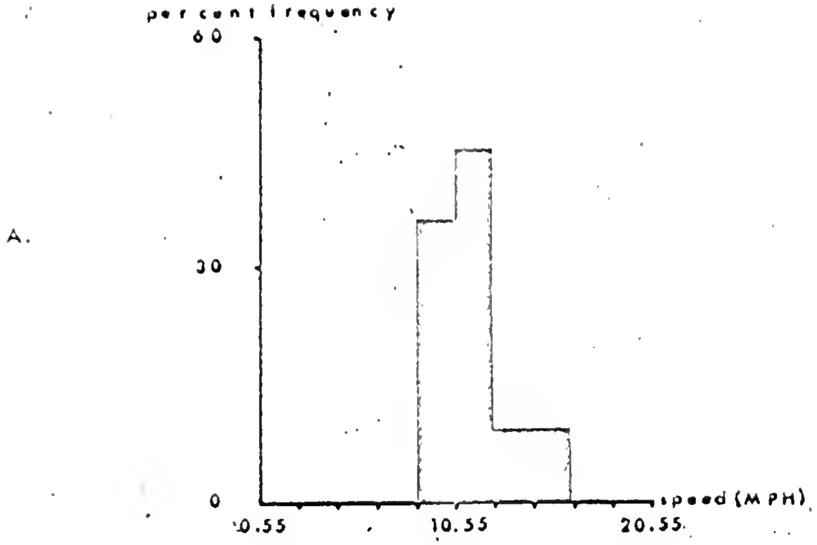


Figure 21. Ground speed of migrants flying against a head wind of 1-5 miles per hour (A) and with a tail wind of 1-4 miles per hour (B).



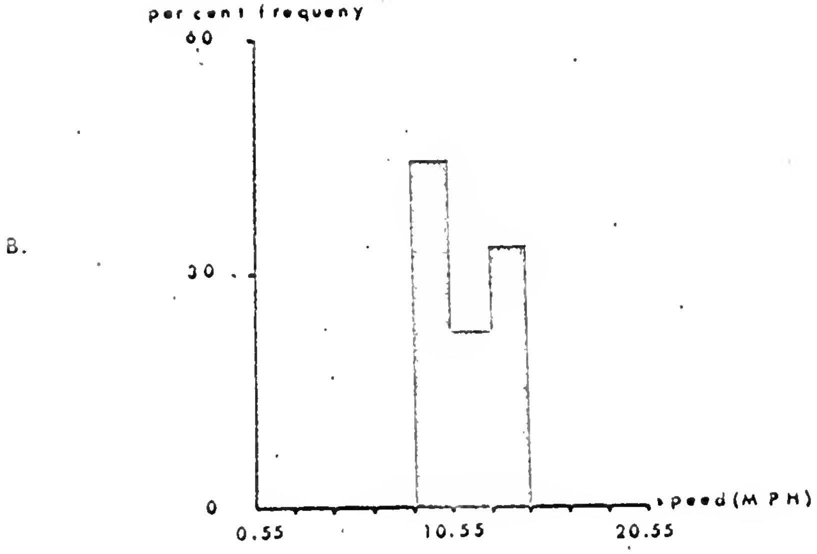


Figure 22. Air speed of migrants flying against a head wind of 1-5 miles per hour (A) and with a tail wind of 1-4 miles per hour (B).

of the 1964 migration are presented in Table 5. The density varies considerably from day to day, but in general, the migration is heavier during the first half of the migratory period. The greatest density observed would be classified as extremely thin according to the scheme of Williams (1958). Wind speed and direction within the limits observed do not seem to affect the number of migrants flying. It appears that cloud cover does not influence the migration density unless the sky is overcast, and then the migration ceases. On four occasions, observations were begun within 1.5 hours after sunrise (Table 6). On three of these days, the day's migration had not yet started when observations were begun. The sky condition was either clear or scattered on all of these days. These data suggest that the time at which the migrants begin flying could be determined by either temperature or light intensity. On September 23, 1964, the sky was clear and the wind was light and variable all day, and observations were made throughout the day. The migratory activity ceased quite abruptly at 1715 EST (about 1.25 hours before sunset). Based on the observations of this day, the migration density does not seem to vary in a regular manner with time of day (Table 7).

Reproductive maturity of the females and sex ratio

Of 43 migrants captured between September 22 and November 7, 1964, 72 per cent were females and 28 per cent were males. This sex ratio is significantly different from 1:1 at the 0.5 per cent level. Since there is no reason to believe that females are more easily captured than males, it appears that while

TABLE 5

DENSITY OF MIGRATION AND WEATHER OBSERVED 1300-1400 EST (1964)

Date	Number Crossing Circle	Density	Sky Cover	Wind	
				Speed	Direction
20 Sep	9	718	Scattered	00-15	360-060
23 Sep	12	954	Clear	00	-------
25 Sep	7	556	Thin Broken	00-07	030-110
29 Sep	3	238	Broken	00-08	100-170
5 Oct	0	0	Overcast	06-19	250-280
7 Oct	1	80	Scattered	05-12	330-060
9 Oct	10	795	Scattered	00-08	360-090
23 Oct	2	159	Clear	03-07	340-110
25 Oct	1	80	Broken	02-09	050-100
7 Nov	3	238	Scattered	00-08	090-190
18 Nov	2	159	Broken	00-06	330-230

TABLE 6

TIME OF BEGINNING OF MIGRATION ON VARIOUS DAYS

Date	Sunrise (EST)	Began Observation		First Migrant	
		Time (EST)	Temp. (°F.)	Time (EST)	Temp. (°F.)
11 Oct 63	0630	0700	53	0930	64-69
16 Oct 63	0632	0800	66	0930	70-73
18 Oct 63	0634	0800	58	0930	65-72
23 Sep 64	0617	0800	67	0815	67-75

TABLE 7

MIGRATION DENSITIES OBSERVED AT VARIOUS TIMES ON SEPTEMBER 23, 1964

Time (EST)	Number Crossing Circle	Density
0800-1000	11	874
1000-1100	11	874
1200-1300	19	1,510
1300-1400	12	954
1400-1500	16	1,272
1600-1700	11	874

the sex ratio is essentially 1:1 in the total population of *Agraulis vanillae*, the females outnumber the males among the migrants. Six migrant females were preserved and dissected. Of these, five had spermatophores in the bursa. Mature eggs were present in the oviducts of three, and in some, the abdomen was partially empty, suggesting that they had already oviposited.

ORIENTATION EXPERIMENTS

Introduction

The ability to maintain a constant compass direction by referring to the sun and compensating for its apparent movement was first demonstrated in bees by von Frisch (1950) and in birds by Kramer (1950). Since that time, this ability has been found in many animals including fish (Hasler, Horrall, Wisby, and Braemer, 1958), amphibians (Ferguson, 1963), reptiles (Gould, 1957), and arthropods (Birukow, 1956; Papi, 1955; Pardi and Papi, 1952), and it has been dealt with in a recent symposium on biological clocks (Long Island Biological Association, 1960) and in a more recent symposium on animal orientation (Autrum, 1963). An animal which is maintaining a constant course by means of this time-compensated sun compass changes its angle with respect to the sun at a rate which is equal in magnitude and opposite in direction to the angular velocity of the sun. This mechanism requires a clock furnishing the exact local time and a knowledge of the sun's angular velocity.

The internal or biological clock which furnishes the local time can be reset, at least in many cases, by subjecting the animals to a light-dark cycle which is out of phase with the natural cycle (Birukow, 1960; Braemer, 1960; Hoffmann, 1960; Pardi and Grassi, 1955; Schmidt-Koenig, 1960), and the amount by which the phase of the clock is shifted depends upon the magnitude of the phase shift in the light-dark cycle. Animals in which the phase of the internal clock has been shifted show a corresponding phase shift in the orientation rhythm. If, for example, an animal which has been trained under the natural sun to search for food in a given direction is subjected for several days to a light-dark cycle in which the light period begins and ends 6 hours later than in the natural cycle, it will search for food 90 degrees to the right of the training direction when tested again under the natural sun. This phenomenon provides one means of demonstrating a time-compensated sun compass in an orienting animal.

Frequently, animals which are orienting by means of a time-compensated sun compass will recognize a fixed light source as the sun and will change their direction during the course of the day by changing their angle with respect to this fixed light source (Birukow, 1960; Braemer, 1960; Kramer, 1952). The rate of change of this angle is such that a constant direction would be maintained if the artificial sun were moving with the angular velocity of the natural sun. This phenomenon provides another means of demonstrating the existence of a time-compensated sun compass.

Methods and Materials

The field observations suggested that the orientation mechanism underlying the unidirectional migratory flight of the gulf fritillary could be a time-compensated sun compass, so two series of experiments were performed to test this hypothesis. In one series, orientation tests were made in a room which was completely dark except for the light provided by a 150 watt flood light serving as an artificial sun. In the other series, orientation tests were made on the roof of a three story building when the sun was clearly visible. The butterflies used in these tests were captured between September 30 and November 7, 1964, at the site used for observations of the migration. They were taken with an insect net while in flight or while pausing to feed at flowers.

The butterflies were tested individually in an octagonal cage with screen sides 24 inches wide and 60.5 inches high, a screen top, and a plywood floor (Figure 23). The top of the cage was divided into eight sectors by four diameters. The butterflies were introduced into the cage by placing them under an opaque container in the center of the floor and then raising the container to the top by means of a string extending to the outside. After the container was raised, they usually remained on the floor for a short time and then flew to one of the sides. Periods of rest, when the butterflies sat motionless with the wings held over the back, alternated with periods of activity consisting of opening and closing the wings while remaining stationary or while walking, and of flying about and into the sides of the cage. The ratio of rest to activity varied considerably from individual to individual and from one time to another in the same individual. Each butterfly was scored by recording its position by sector every 10 seconds during periods

Figure 23. Cage used for orientation tests.

of flight for one hour beginning at the time the container was raised. If an individual was not scored 25 or more times during the first half hour, it was considered inactive, and the test was discontinued.

In the artificial sun experiments, the light was directly opposite the center of one sector. In the outdoor experiments, the center of one sector was aligned with true north so that each sector represented 45 degrees centered about one of the points of an eight point compass. The scores were analyzed using a modification of the method outlined by Papi and Tongiorgi (1963). The direction of the mean vector, θ, and its length, r, were calculated from the distribution of n scores for each individual. The sectors were numbered clockwise from 0-7 beginning with the position of the light, or with north. The direction and length of the mean vector are given by the expressions

$$\tan \theta = \frac{\sum_{i=o}^{7} n_i \cdot \sin i \cdot \frac{360^\circ}{8}}{\sum_{i=o}^{7} n_i \cdot \cos i \cdot \frac{360^\circ}{8}} \quad \text{and}$$

$$r = \frac{\sqrt{\left(\sum_{i=o}^{7} n_i \cdot \sin i \cdot \frac{360^\circ}{8}\right)^2 + \left(\sum_{i=o}^{7} n_i \cdot \cos i \cdot \frac{360^\circ}{8}\right)^2}}{n},$$

where n_i is the number of scores in the ith sector. The direction of the vector is expressed in degrees measured clockwise from the position of the light, or from north. The length is a measure of the dispersion of the scores and varies from 1-0 as the dispersion increases. In the present study, individuals showing values of r less than 0.7 were considered to be disoriented.

Artificial sun experiments were performed on two migrants. The butterflies were confined individually in cubic screen cages 4 inches on a side and kept in a greenhouse under the natural light-dark cycle until they were tested. Observations were made for one hour every other hour between 0800 EST and 1700 EST in one case and between 0900 EST and 1600 EST in the other. The light was located 6 feet south of the center of the cage at a height of 6 feet. Observations were made from behind the light.

Outdoor experiments were conducted between October 18 and November 17, 1964, at Gainesville, Florida. Observations were made from four stations about 3 feet outside the cage, one at each of the four major compass directions, and each station was used for 15 minutes during each test. The butterflies used in these experiments were treated in three different ways. Between tests, the first group was kept under a light-dark cycle which was the same as the natural cycle at the time of year the tests were made. For at least 3 days prior to testing and between tests, the second group was subjected to a light-dark cycle in which the light period began and ended 6 hours later than in the natural cycle. The third group was kept under the in-phase cycle until one or more tests had been made, then subjected to the out-of-phase cycle for at least 3 days and tested again. When they were not being tested, the butterflies were confined in cubic screen cages 4 inches on a side. They were fed once a day as described previously.

The desired light-dark cycles were maintained in controlled photoperiod cabinets in which the temperature was held constant. One of these cabinets is illustrated in Figure 24. It is constructed of ¼ inch plywood on a frame of ½ x 3/4 inch wooden strips and is lined, except for the top, with ½ inch cane-fiber insulation board (Celotex). The dimensions are 26 x 22 x 34½ inches on the outside and 24½ x 20½ x 33-3/4 inches on the inside. Two 24 inch base fluorescent fixtures are fastened inside the top and connected to a time switch (Sears, Roebuck and Co., Model number 5870) on the outside. Lighting is provided by two 20 watt daylight fluorescent bulbs, and the interior of the cabinet is painted white to obtain maximum brightness. The cabinet is partitioned by two panes of double strength glass supported at distances of 11¼ and 17¼ inches from the top by frames of ½ x 3/4 inch wooden strips. Thus the cabinet is divided into a chamber containing the lights, a dead air space between the panes of glass, and a chamber for housing the butterflies. The purpose of the dead air space is to keep to a minimum temperature fluctuations in the housing chamber caused by the light-dark cycle. Access to the housing chamber is provided by a 12 inch high door across the entire front of the cabinet. A strip of ½ inch plywood 1½ inches wide along the top of the door covers the crack between the door and the front of the cabinet to exclude light. Both cabinets were placed in a constant temperature room, and air was circulated through the housing chambers by means of a blower. Air entered through a 2 inch diameter hose

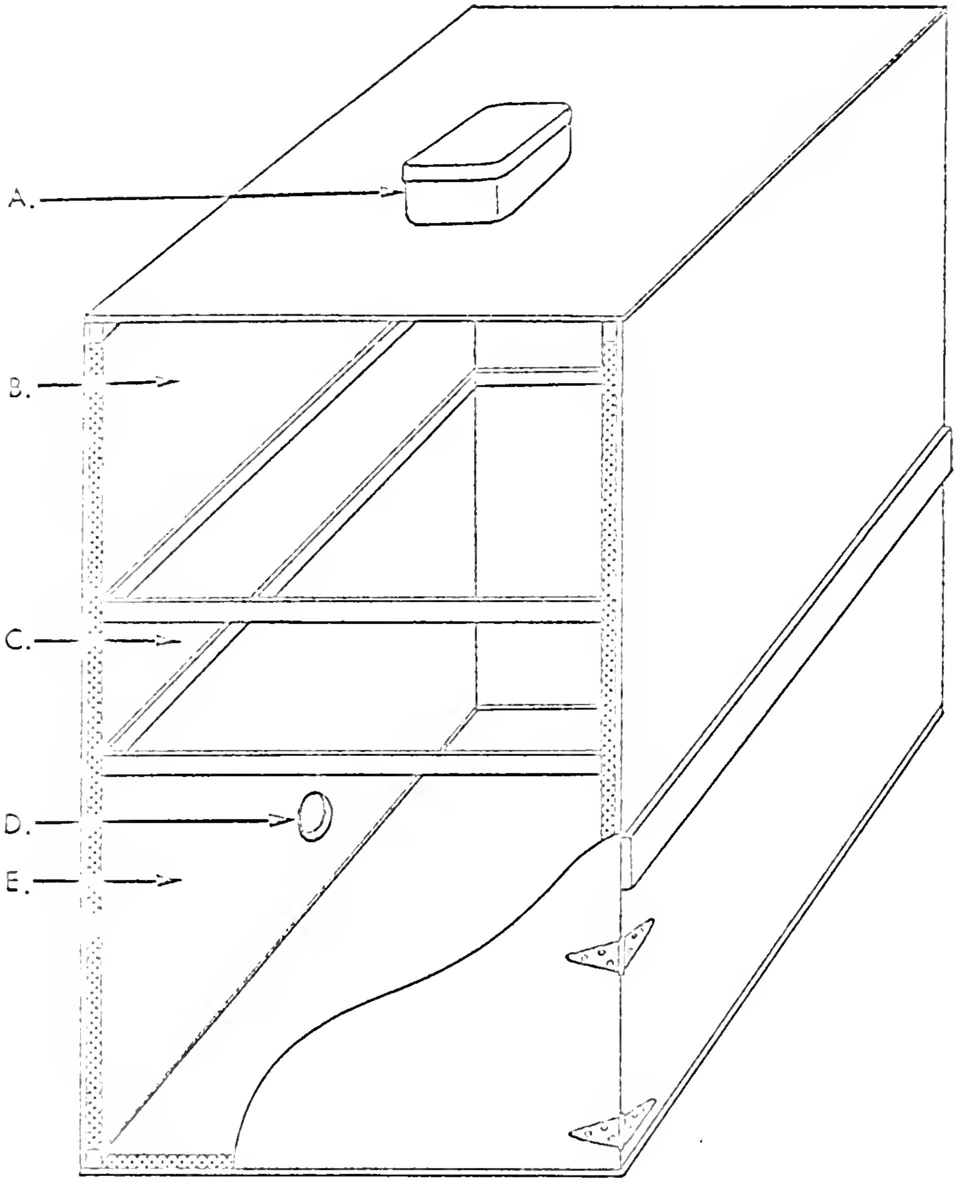


Figure 24. Cutaway view of controlled photoperiod cabinet used in clock resetting experiments. (A) time switch, (B) light chamber, (C) dead air space, (D) air inlet, (E) housing chamber.

in the back of each cabinet and left through a 2 inch diameter hose in the side. Both hoses were curved to exclude light. The temperature in the cabinets varied from 24-25° C. This fluctuation was the same as that elsewhere in the constant temperature room and was not associated with the light-dark cycle.

Results

The artificial sun experiments failed to demonstrate the existence of a time-compensated sun compass. The test butterflies directed their flight activity toward the light throughout the day. The overall illumination in the room was rather low, and it is possible that under these conditions, the compass orientation is replaced by a simple positive phototaxis. Better results might have been obtained by providing diffuse light in addition to the light provided by the artificial sun.

The results of the outdoor tests are summarized in Figures 25-39. In these figures, north is at the top, and the small circle represents the position of the sun at the midpoint of the test period. Each small dot represents a single score, the solid arrow represents the direction and length of the mean vector, and the dashed arrow represents the subjective direction; i.e., the direction the butterfly would be flying if it were maintaining the observed angle to the sun 6 hours before the time of testing. In many cases, the butterfly being tested was inactive, and in nine cases it was active but disoriented. This was probably the result of the repeated handling to which the insects were subjected.

Nine butterflies were active and oriented in one or more tests. When an individual was tested before being subjected to the phase-shifted cycle, it usually flew in the migratory direction whether it was tested in the morning or afternoon (Figures 27, 28, 29, 30, 33, 35). In one case, however, the orientation was reversed (Figures 25-26). This reversal can be accounted for if the model proposed by Mittelstaedt (1960) for the control system of time-compensated sun orientation is accepted.

Some individuals which had experienced the phase shift flew approximately 90 degrees to the right of the migratory direction (Figures 36, 38, 39), while one flew approximately 90 degrees to the right of the reversed direction (Figures 31-32). If it is assumed that under the experimental conditions, the orientation is sometimes turned 180 degrees, as appears to be the case, these results provide good evidence for time-compensated sun orientation.

In the case of Individuals E and G (Figures 34, 37), the mean vector fell in the northwest quadrant after subjection to the phase shift. In both cases, however, there appeared to be a conflict between the reversed migratory direction and the direction imposed by the phase shift. Individual E flew to the northeast for the first 45 minutes of the test period and then to the northwest. Individual G flew to the northeast for the first 10 minutes and then to the northwest. No explanation for this directional conflict is immediately apparent.

The results of these experiments suggest that the migratory direction might be maintained by means of a time-compensated sun compass. While they are too inconsistent to be conclusive, they are suggestive enough to warrant further investigation along these lines.

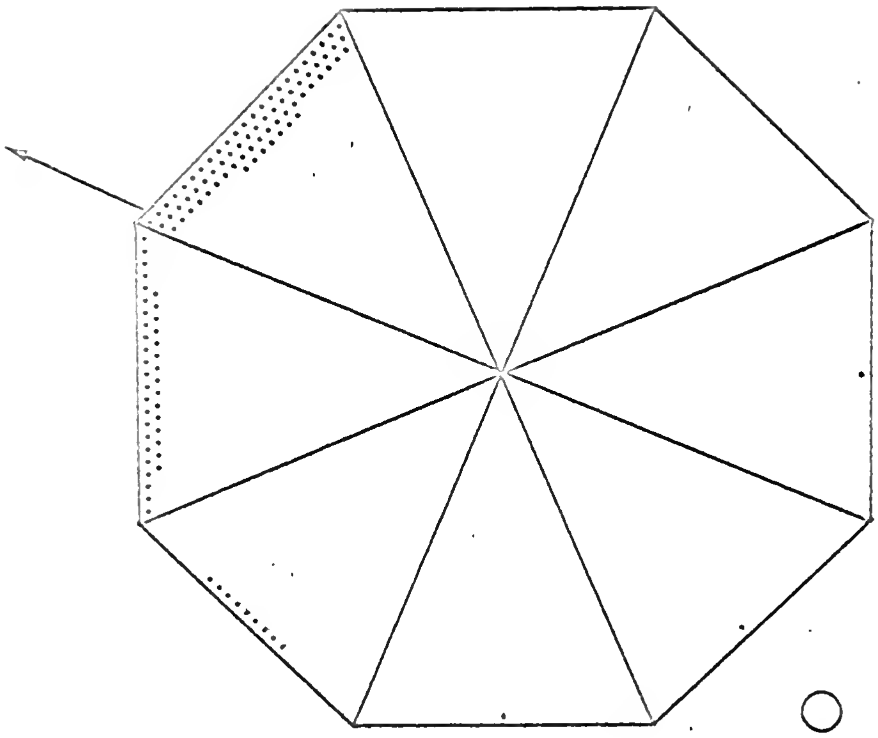


Figure 25. Orientation of Individual A when tested between 0930 and 1030 EST, November 6, 1964, without resetting the internal clock. θ = 295 degrees, r = 0.844.

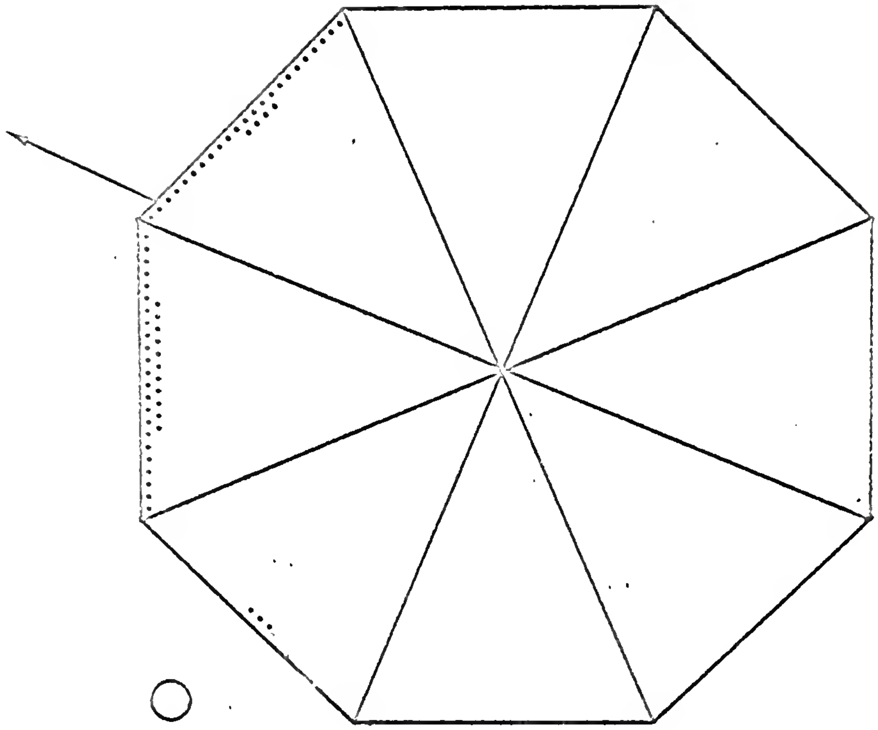


Figure 26. Orientation of Individual A when tested between 1440 and 1540 EST, November 6, 1964, without resetting the internal clock. θ = 296 degrees, r = 0.902.

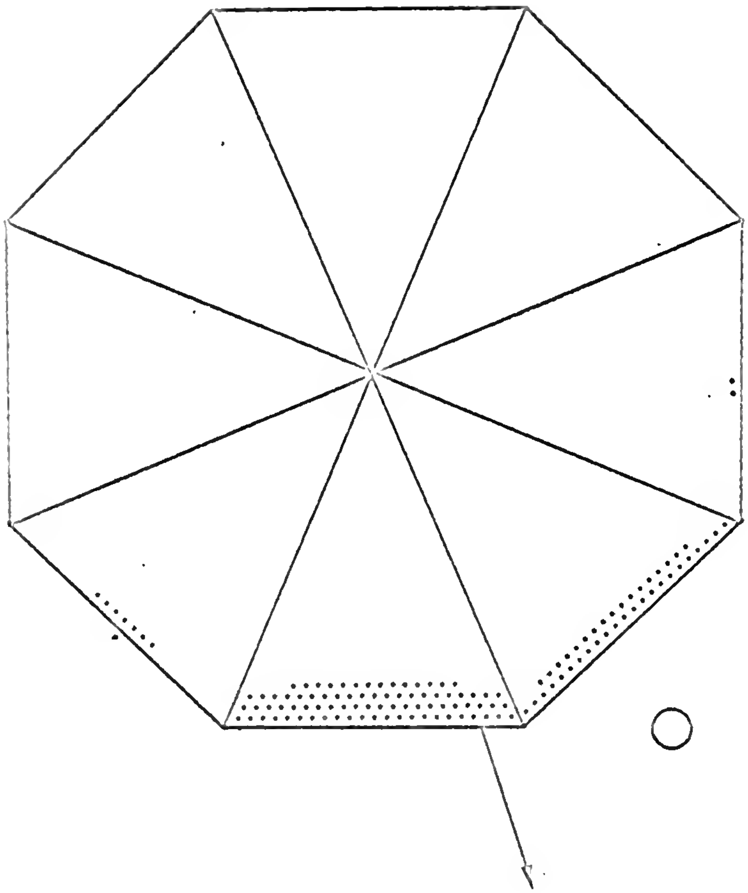


Figure 27. Orientation of Individual B when tested between 0950 and 1050 EST, October 30, 1964, without resetting the internal clock. θ = 163 degrees, r = 0.919.

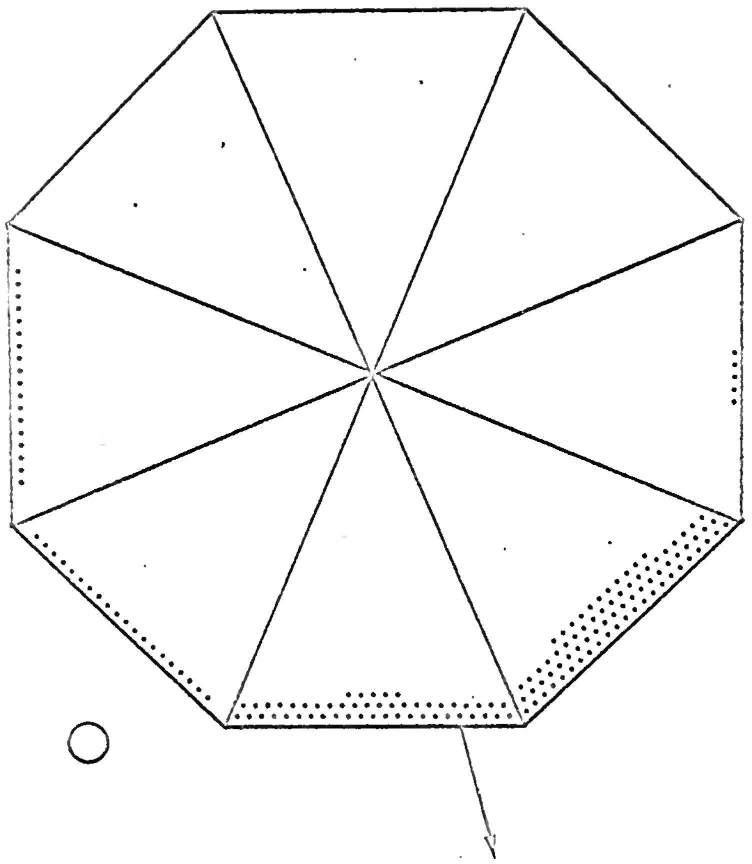


Figure 28. Orientation of Individual B when tested between 1410 and 1510 EST, November 5, 1964, without resetting the internal clock. θ = 167 degrees, r = 0.716.

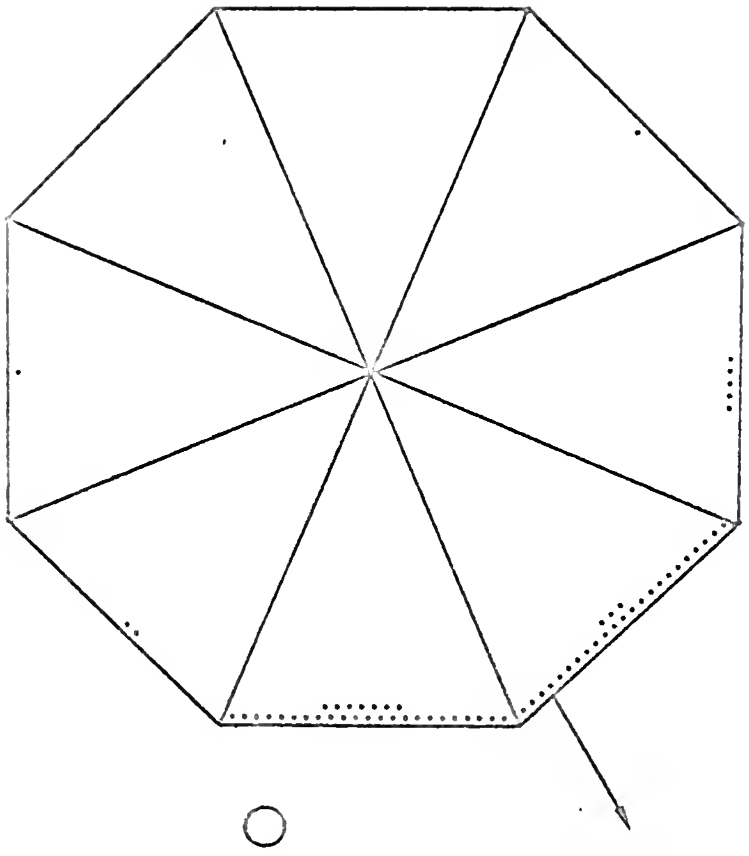


Figure 29. Orientation of Individual C when tested between 1240 and 1340 EST, November 5, 1964, without resetting the internal clock. θ = 156 degrees, r = 0.825.

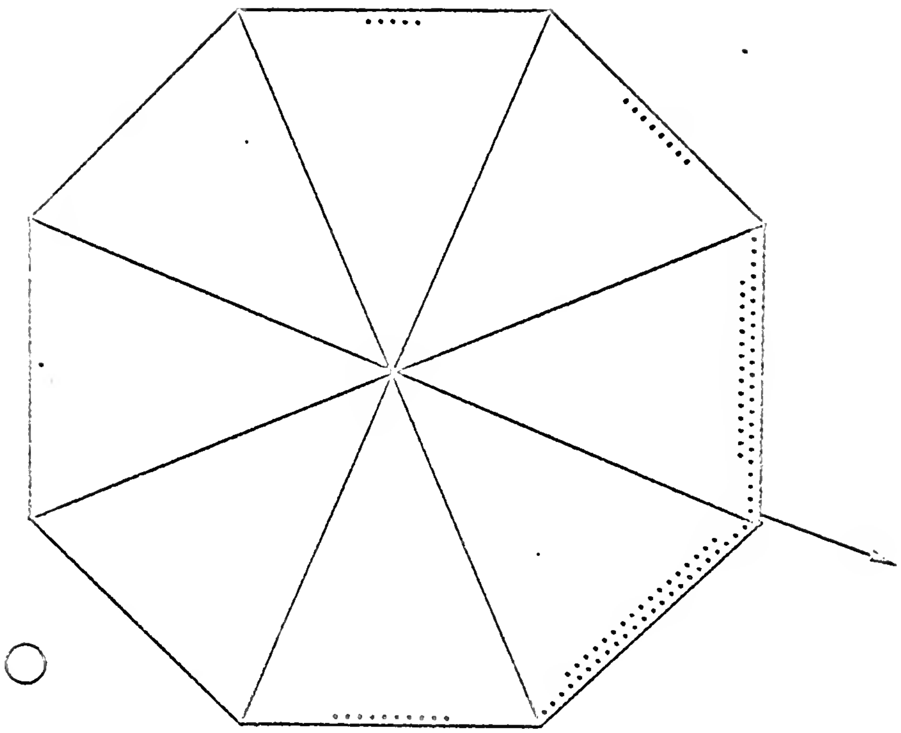


Figure 30. Orientation of Individual D when tested between 1510 and 1610 EST, November 5, 1964, without resetting the internal clock. θ = 111 degrees, r = 0.746.

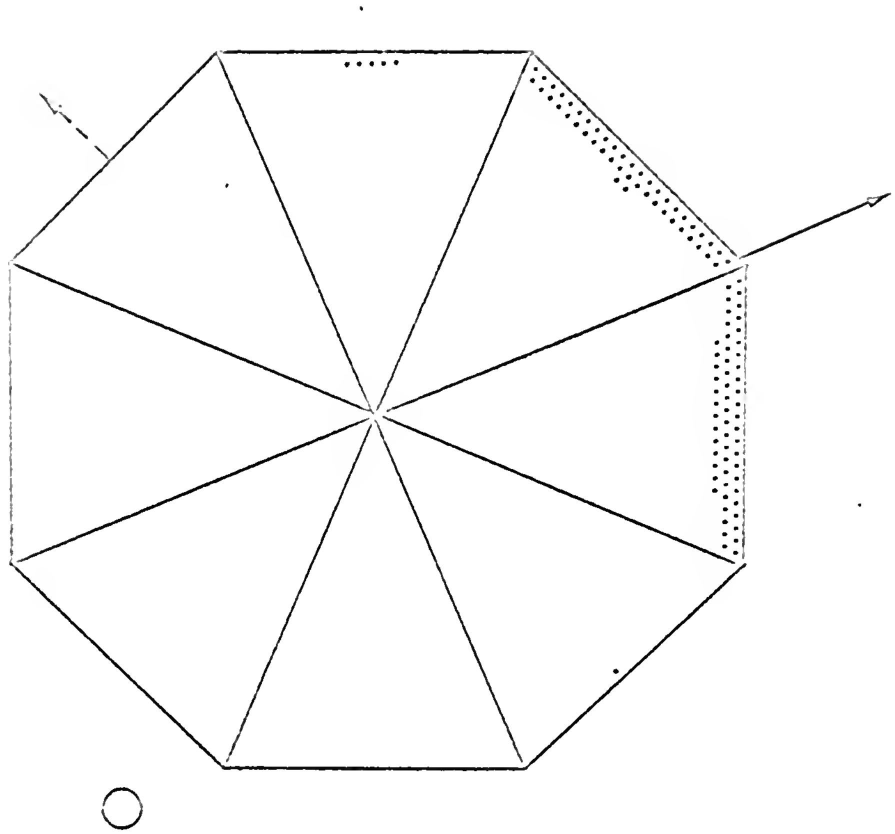


Figure 31. Orientation of Individual D when tested between 1350 and 1450 EST, November 10, 1964, after setting the internal clock back 6 hours (5 days in out-of-phase cycle). θ = 67 degrees, r = 0.853.

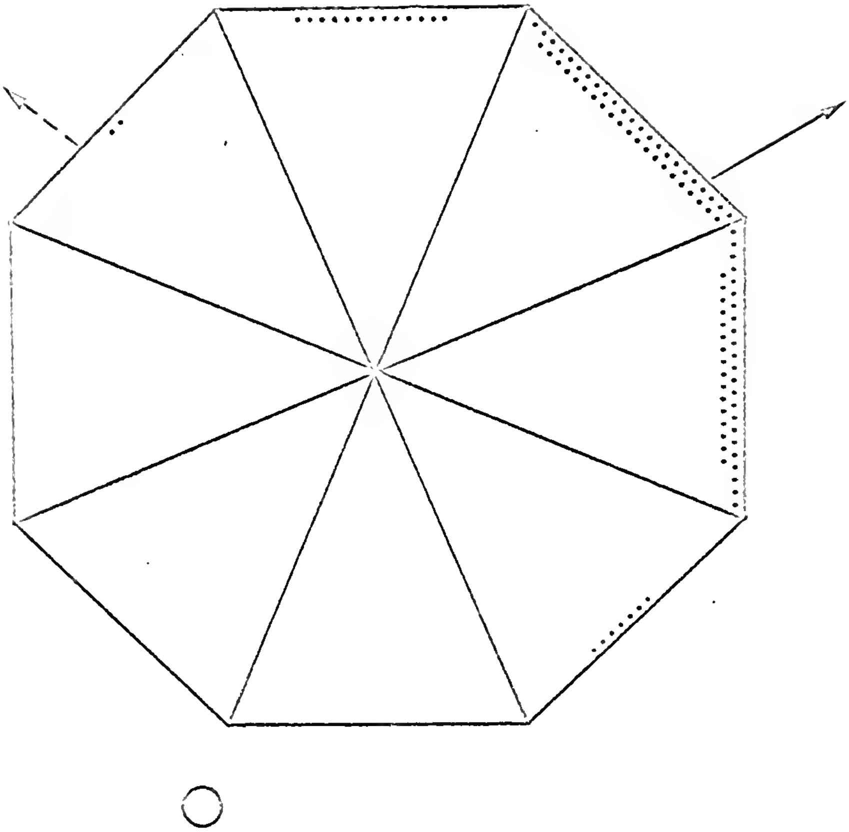


Figure 32. Orientation of Individual D when tested between 1310 and 1410 EST, November 11, 1964, after setting the internal clock back 6 hours (6 days in out-of-phase cycle). θ = 61 degrees, r = 0.801.

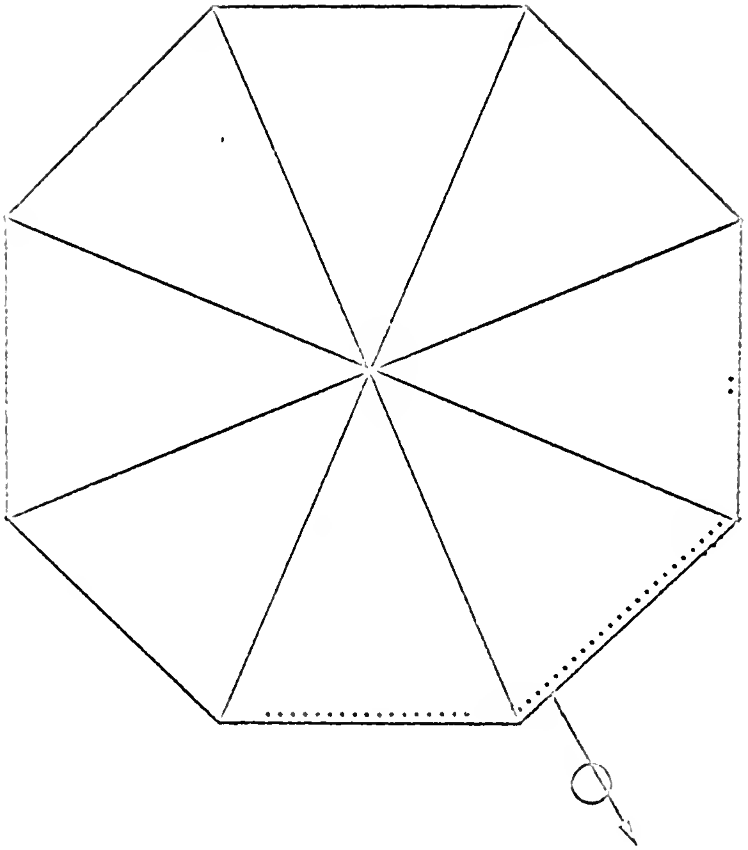


Figure 33. Orientation of Individual E when tested between 1030 and 1130 EST, November 9, 1964, without resetting the internal clock. θ = 151 degrees, r = 0.904.

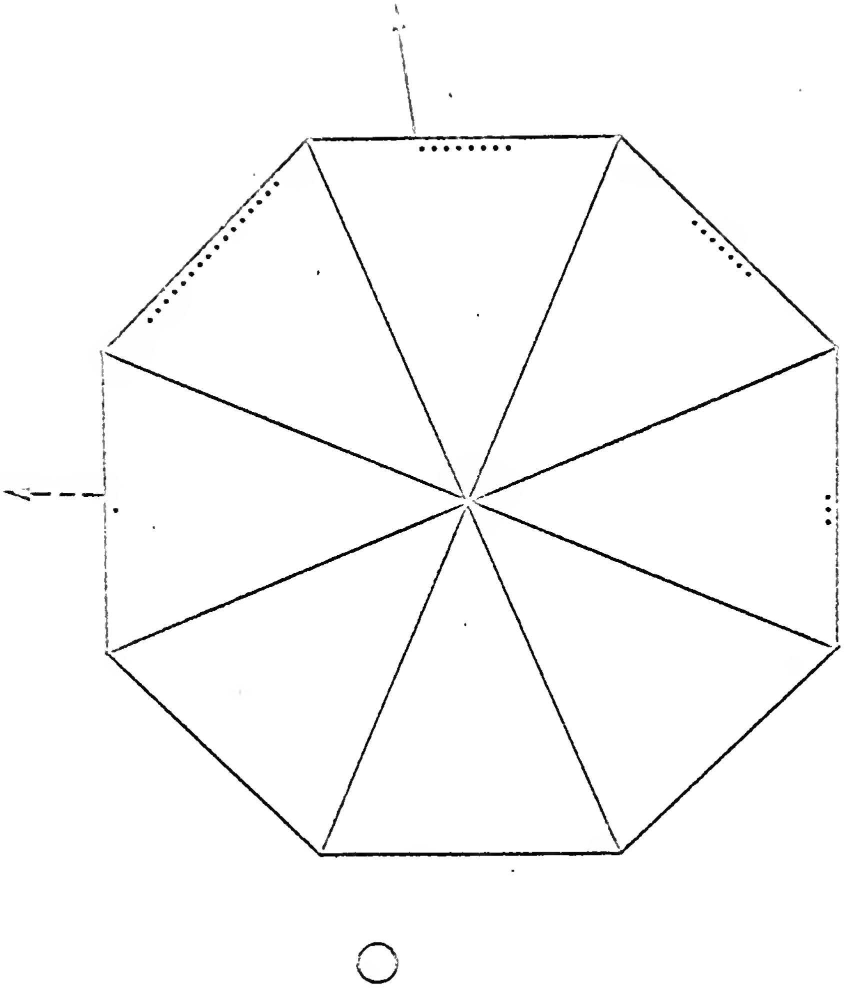


Figure 34. Orientation of Individual E when tested between 1240 and 1340 EST, November 17, 1964, after setting the internal clock back 6 hours (8 days in out-of-phase cycle). Θ = 352 degrees, r = 0.700.

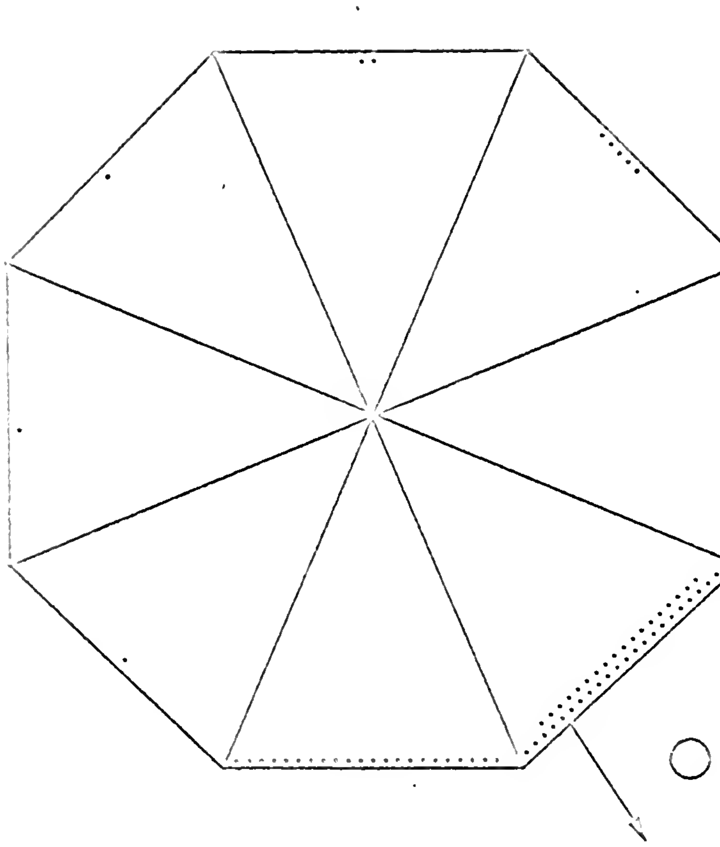


Figure 35. Orientation of Individual F when tested between 0930 and 1030 EST, November 9, 1964, without resetting the internal clock. θ = 138 degrees, r = 0.730.

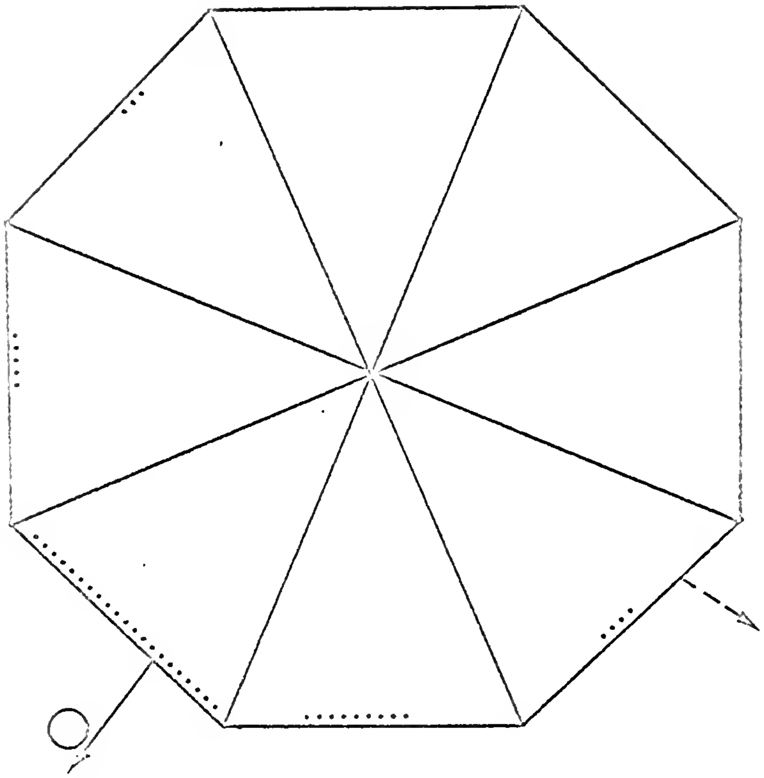


Figure 36. Orientation of Individual F when tested between 1430 and 1530 EST, November 16, 1964, after setting the internal clock back 6 hours (7 days in out-of-phase cycle). θ = 218 degrees, r = 0.741.

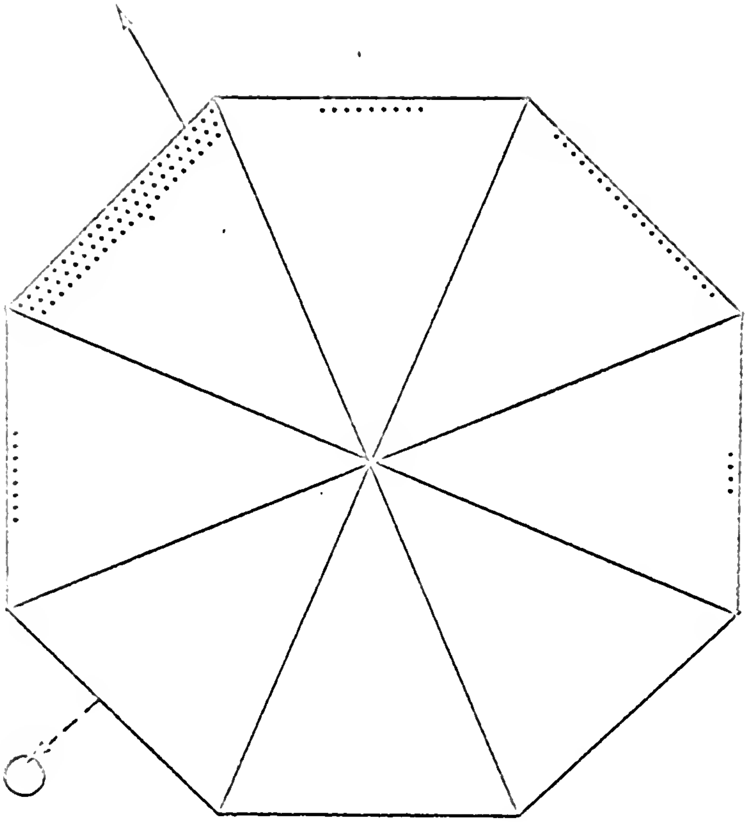


Figure 37. Orientation of Individual G when tested between 1430 and 1530 EST, October 18, 1964, after setting the internal clock back 6 hours (5 days in out-of-phase cycle). Θ = 331 degrees, r = 0.743.

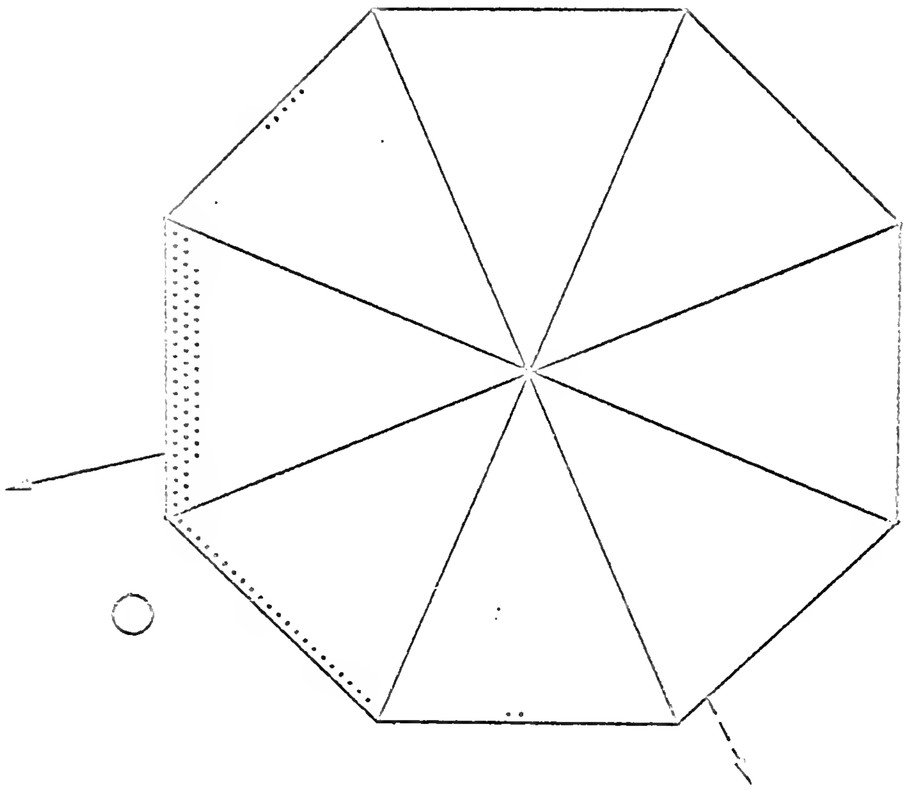


Figure 38. Orientation of Individual H when tested between 1530 and 1630 EST, October 20, 1964, after setting the internal clock back 6 hours (3 days in out-of-phase cycle). θ = 258 degrees, r = 0.903.

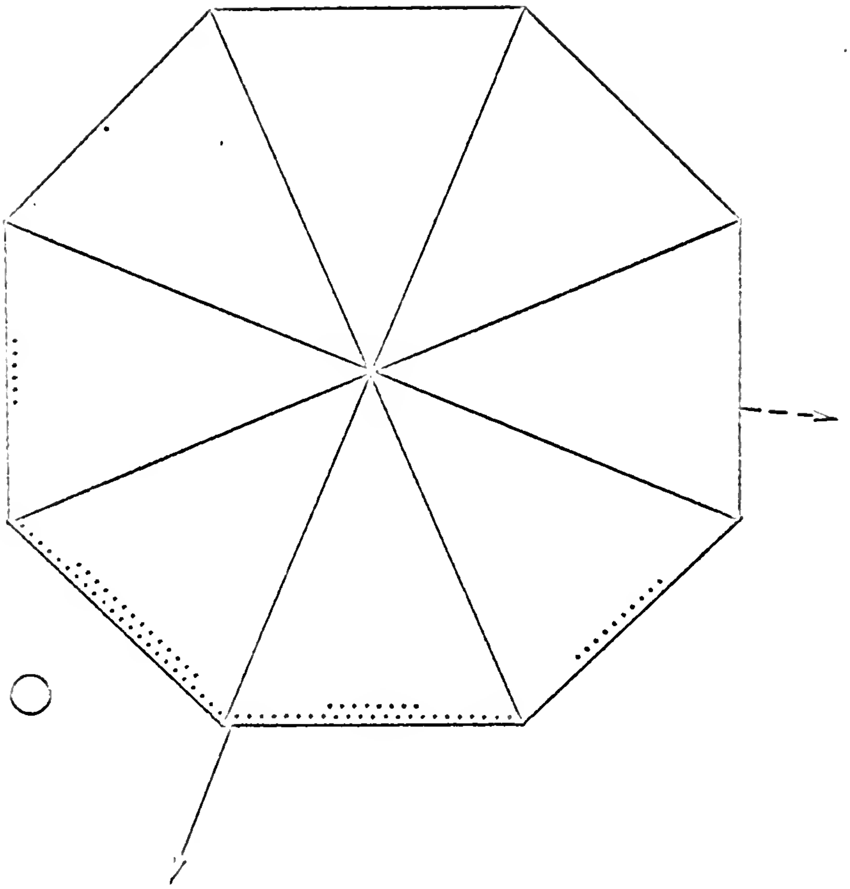


Figure 39. Orientation of Individual I when tested between 1430 and 1530 EST, October 23, 1964, after setting the internal clock back 6 hours (4 days in out-of-phase cycle). Θ = 202 degrees, r = 0.807.

DISCUSSION AND CONCLUSIONS

Southwood (1960) presented evidence supporting the hypothesis that in the course of evolution a low level of migratory activity has been associated with the colonization of permanent habitats and a high level closely correlated with the adoption of temporary ones. The prime evolutionary advantage of migratory movement is the colonization of new habitats and of previously vacated ones. The observations made on the gulf fritillary during the course of this study lend additional support to his hypothesis.

The habitat of *Agraulis vanillae nigrior* is temporary in two respects. First, its relatively small and widely scattered breeding areas are frequently destroyed by the feeding of the larvae or by the depredations of other insects. Second, winter temperatures are too low for its survival over the greater portion of its range. The gulf fritillary is essentially a tropical insect and probably lacks a cold-hardy stage which would enable it to overwinter in these colder areas. At the present time, no precise information is available concerning the cold-hardiness of the various stages or what effect various conditioning factors might have upon this cold-hardiness. Turner (1963) claimed that this insect overwintered for three consecutive winters in west-central Missouri. He based this claim on the fact that the species was quite abundant on Passiflora in this vicinity during three successive summers. This idea was challenged by Howe (1965) who pointed out that females which have traveled from much farther south reach the latitude of Missouri and Kansas during June and July. He also reported that 37 chrysalides kept outdoors in a screen cage during late October in Kansas were all destroyed during a single freezing night.

The observations made during the course of the research reported here suggest that the species is not able to pass the winter even in the vicinity of Gainesville, Florida. If the insect successfully overwintered in this locality, it would probably appear in substantial numbers with the return of favorable conditions. Conditions appear to be favorable for its development by the first of April, but at this time of year it is very scarce and remains so until midsummer. This suggests that the breeding areas in this part of the state are repopulated by females arriving from farther south.

The coastal areas of southern Florida appear to be suitable for the development of the gulf fritillary throughout the year. These localities are less subject to frost than the inland areas due to the moderating influence of water. During the 20 years between 1937 and 1957, less than 25 hours of temperatures less than 32° F. were recorded for an area 0-15 miles wide running along the coast from Palm Beach County to Lee County (Federal-State Frost Warning Service, 1958). Furthermore, field observations showed that both the larvae and the food plants can survive brief exposures to freezing temperatures. It therefore appears very likely that the gulf fritillary continues to breed throughout the winter in these localities and possibly in other warm areas along the Gulf Coast.

At least some individuals leave these breeding sites in the spring and move northward. Apparently the insect is able to maintain only a low population density during the winter, as the northward migration is much sparser than the southward one and is too thin for making measurements of direction and density by means of the technique described earlier. The migrating females apparently lay eggs enroute as patches of the food plant are encountered but do not deposit more than a few eggs in any one locality before continuing their migratory flight. This movement could account for the first appearance of eggs and larvae in the vicinity of Gainesville, Florida, about the first of April and for the appearance of the insect as far north as Kansas and Missouri in June or July. Since the breeding areas are widely scattered, only a few of the females passing through a given latitude will encounter suitable oviposition sites there. Furthermore, since the butterflies are widely separated in time and space, we would not expect all the available breeding sites in a given area to be occupied at the same time. The observations made in the vicinity of Gainesville show that this is the case.

It appears that this migration continues until late summer with the individuals produced in a given locality leaving that locality and moving northward as did their female (and perhaps male) parents. This seems to be the only possible explanation for the low population density which prevailed at Gainesville through most of the summer in spite of abundant food and favorable weather. No evidence was found which suggests that predators, parasites, or disease played a significant role in preventing a population buildup.

At least in some years, the insect reaches the latitude of New York. How far each individual travels before it ceases its migratory flight and leaves the northward expansion of the range to its offspring is a question which can be answered only by a tagging program such as was carried out on the monarch (Urquhart, 1960).

Late in the summer, some of the butterflies begin moving southward. This reversal of migratory direction perhaps appears first in the northernmost segment of the population and spreads southward as the season advances. This movement results in the abandonment of the greater portion of the range. The observations made at Gainesville suggest that not all individuals take part in this migration, but it is unlikely that the descendents of those remaining behind survive the winter. The fact that at least some (and probably many) of the migrant females have mated, have mature eggs in their ovaries, and have partially empty abdomens, strongly suggests that they oviposit enroute. The sudden increase in the size of the egg and larval populations in the vicinity of Gainesville late in the summer could be accounted for by the passage through the area of large numbers of ovipositing females produced in the large northern portion of the range. The estimates of migration density indicate that the southward migration was already at or beyond its peak on September 20, 1964, when the first observation was made. This could also account for the sudden occupancy in August of Area 4 by large numbers of eggs and larvae after it had remained empty during most of the summer. The fact that few adults were ever present in the breeding areas at any one time lends further support to the hypothesis that the eggs were deposited by migrant females. The decline of the populations at most of the breeding sites could be explained by the destruction of food plants, but it cannot be explained in this manner for Area 3. The decrease in all the populations (except in Area 4) is probably related in part to a decrease in the migration density.

The individuals produced from many of the eggs deposited enroute probably reach maturity and move southward themselves before the occurrence of freezing temperatures. Again, the distance traveled by each individual remains to be determined by a tagging program.

The flight direction of the fall migrants passing through Gainesville, Florida, is predominately southeastward. This direction may be affected somewhat by the wind but is not determined by the wind. From the observations presented here, it must be concluded that the direction of the displacement of the population is largely under the control of the insects themselves. If we suppose, as is probably the case, that the flight continues in this direction, the migrants will eventually reach the coastal areas of southern Florida. The fact that A. v. nigrior does not intergrade with the Bahaman and Antillian subspecies A. v. insularis strongly suggests that the migration does not extend beyond the Florida Keys.

The pattern of migratory activity described here is highly adaptive. The northward migration in the spring results in the colonization of new habitats and prevents extensive population buildups in the rather small breeding areas which would result in food shortage and an increase in the rate of parasitism and disease. The northward direction has a distinct evolutionary advantage in that the insects are more likely to find unoccupied oviposition sites in that direction. The descendents of those individuals which migrate southward in the fall survive the winter and repopulate the northern breeding areas the following summer. The descendents of those which do not migrate perish.

Several important problems concerning the migratory behavior of the gulf fritillary remain to be solved. The orientation experiments described here indicate that a time-compensated sun compass may be the mechanism underlying the oriented flight, but the results were too inconsistent to prove this definitely. The best approach to this problem is probably the performance of artificial sun experiments in which diffuse lighting is provided in addition to the light provided by the artificial sun. Experimental work is needed to determine what initiates the spring and fall migrations and how the migratory direction is determined. The most likely initiating factor appears to be either temperature or photoperiod or a combination of the two, but this remains to be proved. Both migratory directions may be genetically determined, one being manifested under one set of conditions and the other under another set of conditions, or the direction may be determined in another manner as it is in the great southern white (Nielsen, 1961). Answers to all of these questions must await future research.

SUMMARY

The larvae of Agraulis vanillae nigrior Michener feed upon Passiflora incarnata L. and probably other plants of the genus, and the adults oviposit upon and in the vicinity of these plants. The insect develops very rapidly, reaching the adult stage in approximately 28 days at 23-24° C. and in approximately 22 days at 28.5-29.5° C. Most adults emerge from the chrysalides during the morning. The females usually reach reproductive maturity 12-18 hours after emergence, and the average adult life span is about 18 days under laboratory conditions.

The adults can be found in almost any open situation, but because of the patchy nature of the food plant distribution, the insect can breed only in small widely scattered areas. The food plants in these small areas are frequently destroyed by the larvae or by the depredations of other insects. Winter temperatures are too low for its survival over the greater portion of its range, but it is probably able to breed throughout the winter in the coastal areas of southern Florida and in other warm areas along the Gulf Coast.

The insect has evolved a migratory habit which has adapted it for the utilization of habitats which are frequently rendered unsuitable for its survival by the depletion of the food supply or by low temperatures. Observations of the fall

migration and of fluctuations in egg and larval populations made at Gainesville, Florida, suggest that there is a northward migration which continues throughout most of the summer, and that the females oviposit enroute. Each individual apparently leaves the locality in which it emerges to participate in this movement. Late in the summer, there is a reversal in the migratory direction which results in at least a partial abandonment of the northern portion of the range.

Observations of the fall migration prove that the migratory direction is independent of topography, time of day, and wind direction. Experiments conducted to demonstrate that the migrants maintain a constant course by referring to the sun and compensating for its apparent movement were inconclusive but were suggestive enough to warrant further investigations along these lines.

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BIOGRAPHICAL SKETCH

Richard Terrance Arbogast was born August 7, 1937, at Freeport, Illinois. In June, 1955, he graduated from Freeport High School. In June, 1959, he received the degree of Bachelor of Science from the University of Illinois. Mr. Arbogast entered the United States Air Force in 1959, and after receiving meteorological training at the University of Chicago, he served in the Air Weather Service until 1962 and was stationed in Arizona. In September, 1962, he was awarded a National Defense Education Act Fellowship for study in entomology at the University of Florida and until the present time he pursued his work toward the degree of Doctor of Philosophy.

Richard Terrance Arbogast is married to the former Helen Dee Fortney and is the father of three children. He is a member of the Entomological Society of America, the Florida Entomological Society, the Lepidopterists' Society, Sigma Xi, Phi Sigma, and Alpha Zeta.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 14, 1965

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Dean, Graduate School

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