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ON THE HABITS OF  
THE MIGRATORY BUTTERFLY  
*ASCIA MONUSTE* L.

BY

ERIK TETENS NIELSEN



København 1961  
i kommission hos Ejnar Munksgaard

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During the first six months of 1949 my wife and I made observations on the habits of *Ascia monuste* as part of a research program in field physiology initiated by Dr. LAURENCE IRVING. Base for this work was at the Archbold Biological Station, Lake Placid, Florida. The basic life-history was worked out, and a number of characteristic elements of the migratory habit were observed (NIELSEN and NIELSEN, 1950).

It seemed likely, however, that a continuation of the study might render a considerably better insight into the subject; and I am, therefore, deeply indebted to the Director and the Advisory Board of the Archbold Biological Station for giving us the opportunity of continuing this investigation for another year. Above all I want to express my most sincere gratitude to the Director, Mr. RICHARD ARCHBOLD, for placing at our disposal all the excellent facilities of the Station, and for all the kindness and help which he and the personnel extended to us.

After this year I joined the Florida State Board of Health to work with Dr. MAURICE W. PROVOST in his research on mosquitoes. It was found that our understanding of the habits of the migratory salt-marsh mosquitoes was considerably enhanced by our previous studies of the butterflies emigrating from the same marshes. As a number of problems relating to the migratory flight of *Ascia* required further study, Dr. PROVOST granted permission to use time, equipment and personnel of the Entomological Research Center of the Florida State Board of Health to continue these investigations in 1954, 1957, and 1960. My best thanks are due to Dr. PROVOST both for his permission to do this work and for his own interested participation in it.

I would also like to cite the names of the many people who in various ways have contributed to this work: Mr. W. L. BIDLING-

MAYER, Mrs. HELEN BOURINOT, Mrs. NINA BRANCH, Mrs. MARILYN CHESSWICK, Mrs. BARBARA DEMPSEY, Mr. W. B. DEMPSEY, Mr. F. SHERWOOD EVANS, Mr. J. S. HAEGER, Mr. JAMES HAEGER, Mr. R. HAEGER, Mr. and Mrs. KARL HODGES, Mr. W. JANSE, Miss KIRSTEN TETENS NIELSEN, Mr. W. PROVOST, Mr. and Mrs. SEXAUER, Mrs. JOAN WOOD, and Mr. W. F. WOOD.

Special mention should be given to Miss HEDVIG TETENS NIELSEN who has taken part in all phases of the work; Mr. L. M. BOURINOT, instrument maker of the Entomological Research Center, for his skillful help in developing the technique which made it possible to mark migrating butterflies; and last, but not least, Mr. FRANK RINALD of the Archbold Biological Station for his help in correcting my faulty English and preparing the manuscript.

This paper reporting on our work on the migratory butterfly *Ascia monuste* is dedicated to the memory of my wife and partner, Mrs. ASTRID TETENS NIELSEN, née SEHESTED.

## I. Introduction

Under certain conditions many insects will become migratory: insect migrations are best defined as a special type of active locomotion by which the individual moves away from its natural habitat. Contrary to birds, insects only once in their life make a migration, and this habit could more correctly be called an emigration. There have only been a few cases reported of a return of the same individual insect to the point of origin.

There is a great variation in the appearance of the migrations in different insects: Aphids migrate only a few meters, locusts hundreds of kilometers; some insects migrate as single individuals and such movements will be detected only by a trained observer, others migrate in countless numbers upsetting the welfare and way-of-living of man. But whatever the appearance of the migration may be, this habit is, according to our present knowledge, always the effect of a basic urge unrelated to other habits. Insects do not migrate for want of food or to fulfill any other direct purpose known to us.

In some insects, such as aphids and locusts, much work has been undertaken to analyse the factors releasing the migratory habit. In butterflies most studies have been simple descriptions of migratory flights reported by stationary observers, a method which is hardly adequate for a penetrating analysis.

## II. Ethology of *Ascia monuste*

### (1) Geographical Distribution

*Ascia monuste* is a pieride butterfly with an essentially tropical distribution. The northern limits of its distribution in Florida vary with meteorological conditions from year to year (fig. 2). The



Fig. 1. *Ascia monuste* feeding on *Bidens*. Slightly dark female on top, male at bottom.



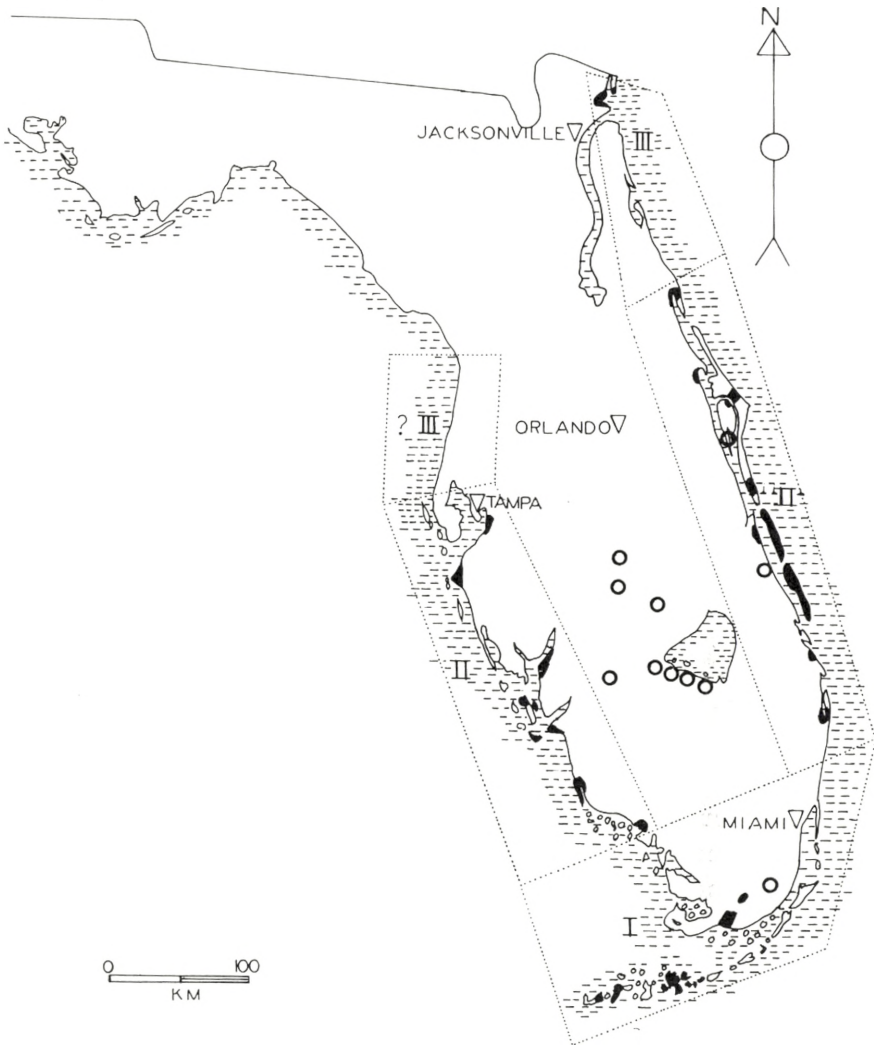


Fig. 2. Sketch map of Florida. The black spots indicate coastal breeding areas; the circles inland populations. "I" is the region of permanent breeding, "II" that of normal breeding, and "III" is the area in which breeding takes place only after a number of favorable years.

average limit approximately follows the line indicating the normal southern limit of damaging frost from Tampa on the west coast running southward to the interior of the peninsula, then following the east coast northward to about St. Augustine. In favorable years populations may be found north of this line; in 1954 breeding occurred on St. Marco Island on the east coast at the border of

Georgia; yet, after a cold winter, very few individuals were found north of the latitude of Miami. The larger, typical populations are always restricted to the coastal area but cross-country migrations following large outbreaks will deposit small, isolated inland populations; a cold winter will wipe out all these small colonies.

Migrations from the permanent breeding areas at the southern tip of Florida eventually re-establish the populations further and further north; the process takes about three or four years before "normal" conditions again prevail. *Ascia monuste* has always been found to breed in well-defined colonies. The formation of more or less isolated populations is caused by the presence of the plants on which the larvae feed. Along the coast, where all the large colonies were found, the larval food plant was *Batis maritima* (Family *Batidaceae*), which grows 30–50 cm tall. The stems tend to sprawl and the succulent leaves have a salty, spicy taste, and a characteristic odour. Usually the plants form a dense cover over vast areas of tidal marshes and under black mangrove. Even where *Batis* covers scores of acres, its occurrence is limited to parts of the coast and alternates with other types of vegetation on which *Ascia* larvae do not feed.

The second most important food plant is peppergrass (*Lepidium virginicum*), a small wayside weed of the family *Cruciferae*. Occasional occurrence on *Tropaeolum* in gardens, *Cleome*, *Cakile*, and (only in one case) cabbage, complete the list of host plants (NIELSEN and NIELSEN, 1950). Usually these populations are very small; during several months we followed a colony based on a patch of peppergrass where the normal number of imagines was about six.

In the following part the composition of the colonies will be discussed in more detail, but it is very essential to the understanding of the behavior of *Ascia*, and especially of the migrations, to keep in mind that these animals are distributed in discrete units based on the limitations of the breeding areas.

## (2) The Egg

The egg and the egg-laying was previously described in some detail (NIELSEN and NIELSEN, 1950). It was observed that the eggs were laid singly or a few together on the commonly used foodplants (*Batis* and *Lepidium*), while the were deposited in

clusters of up to 50 on the broad-leaved plants such as *Tropaeolum* and *Cleome*. In 1954, during the very heavy outbreaks on the east coast in 1954, eggs were found on *Batis* in large numbers, sometimes 30–40 on a single plant. Such eggs were, however, not arranged in neat clusters but scattered in different directions. They were undoubtedly laid on different visits, probably by different females. Females were observed not to lay more than a few eggs before moving to another plant.

The tendency, previously noticed (NIELSEN and NIELSEN, 1950, to deposit the eggs on small specimens of the food plant was also confirmed. In the salt marshes the eggs were usually found on smaller *Batis* plants, 15–30 cm high, growing under the cover of taller ones. When the eggs were laid on taller plants it was usually where there was shade from higher vegetation such as black mangrove. They were of course easier to see here, and when inspecting such a locality for eggs we would first examine *Batis* plants under a mangrove tree. The eggs were often situated so low that occasionally they must be reached by tides. In the laboratory we immersed eggs from time to time, and also kept them constantly moistened with salt water; in neither case was the hatchability of the eggs impaired.

In an orange grove on Lotus Island between Georgiana and Honeymoon Lake, a dense stand of tall *Lepidium* grew in the open spaces between the rows of orange trees, but neither eggs nor larvae were found here. Under the trees, however, grew a dense stand of various weeds and under this vegetation were tiny peppergrass plants. Eggs and larvae were found on these peppergrass plants and pupae on the weed growth above them.

The duration of the egg stage was observed in several cases, both with eggs laid in the laboratory and those we have observed being laid in nature and brought into the laboratory. There was considerable individual variation in the duration of the egg stage under uniform conditions, and this variation or dispersion seemed proportional to the duration, or even relatively greater the longer the duration. At 27° the duration was 84 hours and the dispersion from the first to the last hatching was two hours or about  $2\frac{1}{2}\%$  of the duration; at 19° the eggs hatched at an age of 180 hours and the dispersion was found to be eight hours or  $4\frac{1}{2}\%$  of the duration.

The results of the experiments, in which 274 eggs were used,

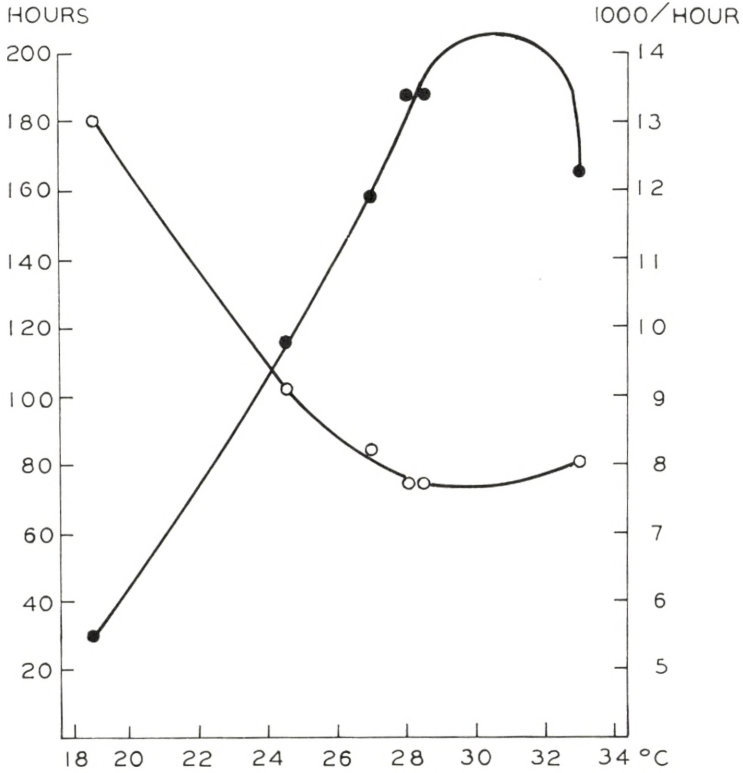


Fig. 3. Duration and velocity of the egg development of *Ascia monuste*.

are shown in fig. 3. The relation between temperature ( $t$ ) and velocity of development ( $v$ ) was probably of the usual form:  $v = a + b \cdot c^t$  (NIELSEN and EVANS, 1960) but the material hardly permits a detailed analysis. Temperatures above  $30^\circ$  are unfavorable, in good agreement with the observation that shaded places were preferred for the deposit of eggs.

In one experiment at  $28.5^\circ$ , 15 eggs were kept at 90 % relative humidity and ten eggs from the same batch at 60 % r.h. The mean durations were 75 and 74 hours respectively, and variation within this range of relative humidity seemed thus not to have any influence on the egg stage.

### (3) The Larva

The hatching of the eggs was preceded by changes in the embryo visible from the outside. From 10 to 20 hours before the hatching (depending on the temperature) it was possible to discern the eyes of the larvae and during the last four to eight hours a number of hairs were seen. It usually took the larva one to two hours to gnaw an opening in the shell.

In the first report (NIELSEN and NIELSEN, 1950) it was stated that there were at least four larval instars; the actual number is five. The head capsules of five larvae from the same batch were measured twice a day. Assuming that I, II, etc. indicates the head widths of the five instars, the ratio II/I was 1.67, III/II was 1.65, IV/III was 1.58, and V/IV was 1.52.

For easier inspection these larvae were kept in the laboratory at room temperature which varied between 26° and 30° with a mean of 28°. It was therefore not possible to determine the duration of the single stages with any degree of accuracy. The first three instars were of about the same duration, 10–15 % of the total each; the fourth instar was about 20 %; and the last instar, about 40 % of the total duration.

DETHIER recently (1959 a, 1959 b) discussed the importance of the availability and distribution of food plants for a butterfly population. This is hardly a problem in the marshes where there is a practically inexhaustible and uniform supply of *Batis*, but it could easily be important for the small inland populations.

It is well known that before pupation the larvae make large roving excursions; similar activity takes place on a smaller scale before each moult, and often—or perhaps even usually—they end up on a new food plant.

The total duration of the larval life varied considerably. All our experiments were made at 24–29° and it is impossible from our data to show the influence of temperature. Larvae from eggs laid within the same eight hours pupated from an age of nine to more than 14-days old (fig. 4). They were kept at a fairly constant temperature of about 24°, had the same food and were rotated on the shelves to compensate for local differences in temperature. In the duration of larval life no differences were found between the sexes. Crowding had no effect on the duration of larval life.

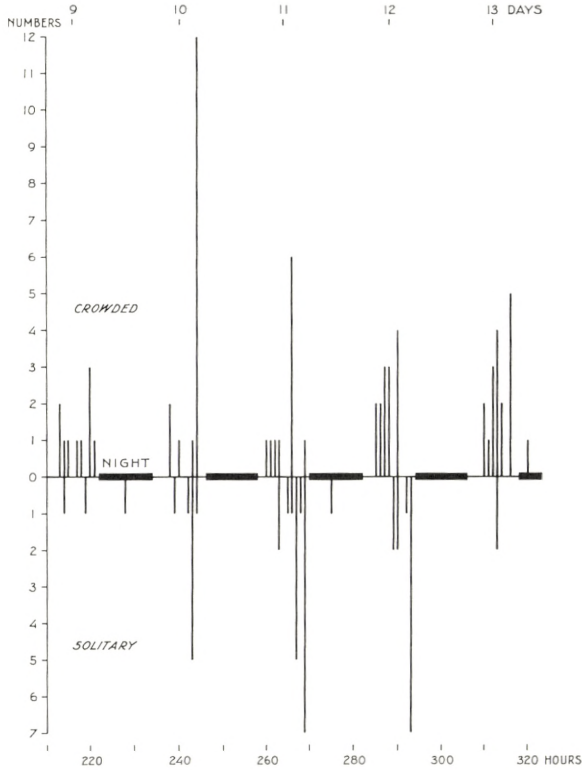


Fig. 4. Duration of the larval stage in *Ascia monuste*. The abscissa is the age at which the pupation took place, given as days (above) and hours (below). The ordinates are the number of pupations of crowded larvae (upper part) and solitary larvae (lower part).

#### (4) The Pupa

Fig. 4 and also fig. 5 show that pupation is almost entirely restricted to daytime with a very pronounced maximum towards the end of the day.

One, or sometimes two, days before pupation, the larva stops eating and moves around all day. In the field this activity will usually bring the larva to a fairly high point above ground usually more than one meter, sometimes 3–4 meters, e. g. on a twig or a leaf. Finally the larva fixes itself to a certain place to be used as a base, often vertical; if sloping the underside is usually preferred.

The shoe-like support for the abdomen is first spun, after

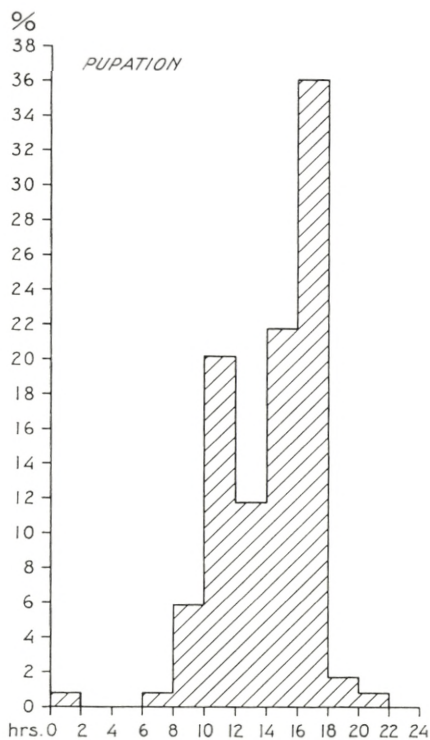


Fig. 5. Distribution of pupations of *Ascia* over the 24 hours.

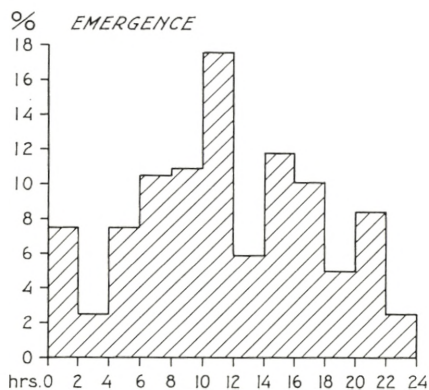


Fig. 6. Similar distribution of emergences of imagines.

which the animal turns around and fixes the tip of the abdomen into the shoe. The thread over the thorax is then made. With the front part of the body curved back nearly  $180^\circ$ , it fastens a thread on one side of the body. While continuously spinning, it moves the head to the opposite side and fixes the thread there. This is repeated until the thread is strong enough. During this process the larval body already begins to shrink in length and increase in width; after a couple of hours it has almost the normal shape of a pupa. There might still remain a long period—often overnight—before the larval skin is shed. For a few hours the coloration remains larval, after which it gradually changes to that of the typical pupa. The color of the pupa depends on the background (NIELSEN and NIELSEN, 1950).

The duration of the pupal stage is 6–7 days at  $28^\circ$ , and 7–8 days at  $25^\circ$ . No differences were found in the duration of the pupal stage relating to the sex of the adult or crowding of the larva.

### (5) Emergence

Males and females emerged in approximately the same number in the breeding experiments; of 210 cases 100 were females and 110 males. There was no evidence either in the field or in the laboratory that one sex emerged before the other.

When pupae were kept in daylight there was a maximum of emergences during the daytime between 09<sup>h</sup> and 17<sup>h</sup>. Of 31 individuals, 7–9 % emerged during each of these hours against 2–4 % during the remaining 19 hours of the diel.

In another series of experiments the larvae were kept in daylight and the pupae were in a temperature controlled room with artificial light which was on most of the time. Under these conditions the emergences were more equally distributed although most of them occurred in the daytime (fig. 6).

### (6) Sexual Development of the Female

As it was found that migrant females normally have immature ovaries, dissections were made to find at what age the eggs became mature. ZAHER and LONG (1959) found that crowding affects the duration of the preoviposition period, and the animals were therefore kept either crowded (C) or solitary (S). In the following these letters are used to indicate the condition of either larva (first letter) or imago (last letter): CC, CS, SC, and SS.

In a preliminary experiment with 12 females it was found that no development took place until the females were about 24-hours old; and in the second experiment, the females were killed at an age of 23 to 46 hours.

The results are given as fig. 7. There seemed to be a slight delay in the development of the females which were kept crowded as larvae but the dispersion was too large to permit any definite conclusions to be drawn. Some of the females of all four groups remained immature after more than 40 hours.

In the virgin female, bursa copulatrix has a peculiar dented shape. The spermatophore is round with a pointed stem; it swells the bursa to a ball shape. Later, the spermatophore empties and bursa deflates again to the dented form. Sometimes two spermatophores are found in bursa; in one case even three.



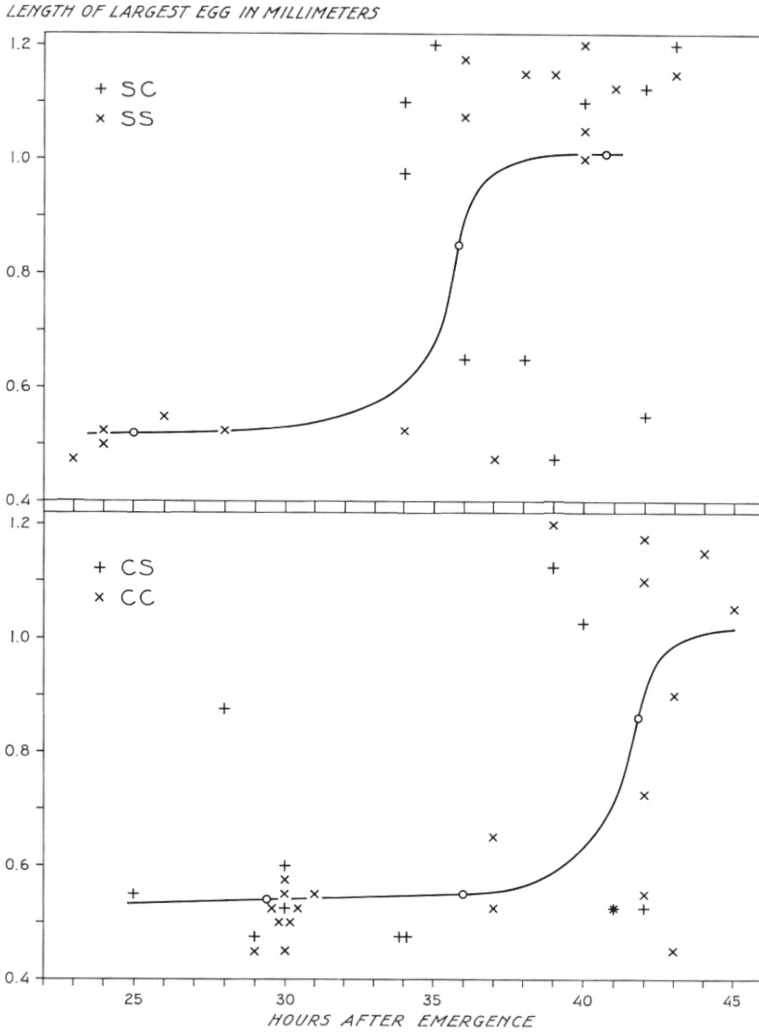


Fig. 7. Ovarian development in crowded and solitary *Ascia*.

- SS: Solitary all life
- SC: Solitary as larva, crowded as imago
- CC: Crowded all life
- CS: Crowded as larva, solitary as imago

### (7) Copulation

In nature copulation is usually preceded by a series of complicated maneuvers. In the first stage male and female fly close together for some time, the flight becoming faster and faster until

a special whirling flight is adopted. The two animals encircle each other and at the same time each seems to try to rise above the other with the result that the participants are propelled higher and higher in the air. This stage ends in the female alighting, often on a leaf up in a tree or on a palm frond, sometimes after a sudden drop to the ground on a low weed or a bush, or even on the ground.

Contrary to the normal position the female now keeps her wings spread horizontally. The abdomen is exposed and raised and lowered in a sort of waggling movement. With very fast wing beats the male hovers behind and a little above the female, now and then darting towards her until he finally succeeds in seizing her. Very often the female flies away before that happens and the whole procedure may be repeated several times.

Copulating *Ascia* fly around as if they were single individuals, the female often visiting flowers. Usually the copulating pair disappear from view before they separate, but it is not unusual to see the same two animals united for ten minutes or more. Actual coitus has not been observed.

When not feeding on flowers, the males mostly fly around in the breeding area among the food plants, apparently trying to find females. When many males are present, as during the large outbreaks, males frequently copulate with females just beside the empty pupa-skin from which they emerged, the female's wings still soft and unable to carry them in flight. In such cases there cannot have been any introductory flight.

### (8) General Activity

Limitation in the freedom of *Ascia* caused a general inhibition of most of their normal behavior. At the Archbold Biological Station a huge open-air insectarium was built to house a colony of them; a screened cage 150 cm enclosed a 3 × 7 m flower bed with *Tropaeolum*, a favorite food plant, with eggs and larvae. When the butterflies emerged their only reaction was to try to escape; all day long they fluttered against the screened ceiling, disregarding the birds which soon picked them out through the screen. In smaller cages even the escape reaction disappeared and the animals were usually rather apathetic. Our efforts to

measure the spontaneous muscular activities by means of an actograph were therefore unsuccessful.

*Ascia* do not always eat voluntarily in captivity. There was considerably individual difference in the "docility" of the experimental animals. They were fed each morning and sometimes also in the afternoon. Some of them stopped eating after a little, others had to be removed before they had eaten too much. After a meal during which one of the butterflies was left to eat as it pleased, its weight had increased from 83 mg to 122 mg, and the abdomen was dilated to an extent never seen in nature.

### (9) Longevity

The longevity of the adult *Ascia* is very important to an understanding of its behavior, and especially of the migratory behavior of butterflies. In the laboratory females normally live seven to ten days; there were two exceptions, one lived 12 days and the other 16. The male has a normal lifespan of six days and none lived more than eight days. Individuals caught in nature usually died after a couple of days; very fine specimens of females with perfect scales and wings would live up to a maximum of seven days; comparable males five days. There is no reason to believe that the conditions of captivity caused the butterflies to die prematurely. In captivity they do not waste energy on the stresses of normal life and are protected against enemies. In nature many individuals succumb to predators: ambush-bugs (*Phymata erosa*), lizards, birds, and dragonflies, in decreasing order of importance. In the many cases, where the animals feed along highways, a considerable number are also killed by cars. In the following (p. 32-33) shall be mentioned that the longevity in the field is the same as found in the laboratory.

### (10) Variability

Of the several varieties of *Ascia monuste* we observed only the form *phileta* in which the female is dark in the summer instead of white; the male is white in all seasons.

During the first part of this work we saw only dark females migrate and for some time considered it as a "migratory phase". With our permission, Dr. ALEXANDER B. KLOTS used this infor-

mation in his book "Field Guide to the Butterflies" (1951). Later on it was found that the white females also migrate. I deeply regret misinforming Dr. KLOTS, and I alone am to be blamed for having brought this error into his excellent book.

From November to February all females are white. In 1950 the first dark ones were observed in the last part of February during an outbreak at Boynton Beach. At Fort Pierce the first dark females were seen on March 16, but it was not until April 19 that it was possible to distinguish males from females by color without catching them. Mr. and Mrs. KARL HODGES reported the first dark females in Indialantic, near Melbourne, on March 24. A northbound migration from Titusville, March 28–29, had several dark females, while a simultaneous southbound migration from New Smyrna Beach had only very few. The return to the typical form was not followed closely, but in 1949 it took place during October.

It is remarkable that the change to *phileta* came later in the northern part of the east coast than in the southern. Along this stretch of the coast, about 300 km, there is a considerable difference in temperature; the mean temperature for January is 20° at Boynton Beach, 18°5 at Fort Pierce, and 15°5 at New Smyrna. Eggs laid in December and January and developed at 28°–29° resulted in females as white as their parents; and in August a brood developed to dark females at 20°. Early in February 1960, eggs were taken into the laboratory and developed at 24–26°. The butterflies appeared the first days of March; most of the females were tinted, and about half of them were dark. In the field the same brood was retarded by cool weather and appeared first on April 3. The females were in the same transition stage of coloration as those reared in the laboratory. HOWANITZ (1948) studied the differences in the ecology of several varieties of *Colias*, but that variation was probably of another kind than the dimorphism in *Ascia monuste*.

### (11) Preferred Temperature

To obtain a better insight into the effect of temperature on these butterflies a number of determinations of the preferred temperature were made. (NIELSEN and NIELSEN, 1959).

It was found that there were variations in the preferred temperature according to season, sex, conditions of feeding, and possibly to time of the day.

### III. Populations of *Ascia Monuste* L. on the East Coast of Florida

#### (1) Description of the Observed Populations

The Atlantic coast of Florida is characterized by a long row of narrow islands, a sort of offshore bar, often simply called "the Beach" (figs. 8 and 9). It is separated from the mainland by a lagoon which in different sections had different names, e. g. Mosquito Lagoon, Indian River, Lake Worth. A typical cross-section of the coast is given in figure 4. Further details of topography, soils, vegetation, etc., may be found in the book by KURZ (1942).

Both in the mangrove and in the open salt marshes on the west side of the bar *Batis maritima* is a typical plant; it also occurs on the mainland. Most of the flowers on which the adult butterflies feed are found in the region behind the dunes and along the roadsides. Among the more important are the composite *Bidens* sp. and *Helianthemum arenicola*, also such shrubs as *Lantana involucrata* and *Coccolobis uvifera*, and weeds like *Vigna repens*.

Although the butterflies in the breeding areas may visit the mangrove and the composite bush, *Borrchia frutescens* when in flower, they ordinarily move to the roadside flowers to feed. This differentiation of the territory of *Ascia* into a breeding area and one in which the adults forage is characteristic for the coastal populations. As the feeding areas are usually concentrated along the beach roads these places offer a favorable opportunity for inspections and counts of the populations. From the spring of 1950 we concentrated on the middle east coast of Florida as the most convenient area for the work.

Following is an annotated list of what we believe to have been all the important populations between New Smyrna Beach (29°00' N.) and Boynton Beach (26°30'); which is to say, along 300 km of Florida's east coast (fig. 8).

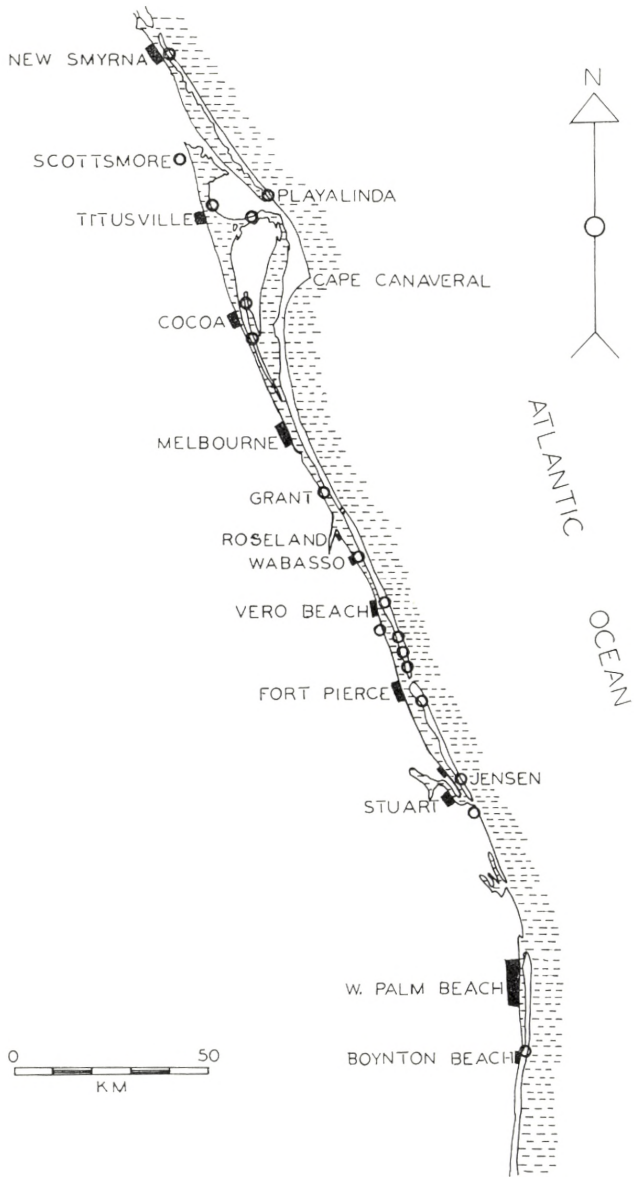


Fig. 8. Sketch map of part of the East coast of Florida. Circles indicate breeding areas. Black squares are cities.

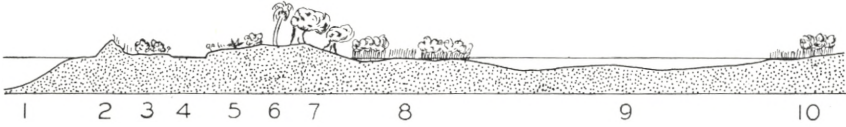


Fig. 9. Diagram of a cross section of the offshore bar and lagoon on the East coast of Florida.

1. The Atlantic Ocean
2. Dunes
3. Weeds and bushes as *Lantana* and *Coccolobis*
4. The road A1A
5. Roadside flowers and scrubs
6. Palms
7. Oak wood
8. Mangrove and salt marsh
9. Lagoon
10. The mainland

The descriptions refer to the situation in 1949–1950; the increasing house building, re-arrangements of roads, impoundments and destruction of the natural vegetation by sand-dredging and other so-called developments are rapidly changing the coastal area to such a degree that several of the points mentioned below no longer can be recognized.

### *New Smyrna Beach*

This was one of the main outbreak centers formerly observed by FERNALD and others. FERNALD (1937 a) had the impression that the butterflies came from the interior of the peninsula, and a little north of New Smyrna on the mainland there was a possible breeding area around Turnbull Bay; the bay penetrates the mainland with areas of mangrove and *Batis* along it.

Only once did we observe an outbreak here, in March 1950, coming from the salt marshes on the islands which here nearly completely fill the lagoon.

### *Titusville Area* (map, fig. 10)

Here there were two smaller populations in open salt marsh, one at the bridge to the mainland and one north of the bridge to Merritt Island. In the salt marshes as Playalinda there were many patches of mangrove, and the enormous breeding area there comprised several types of vegetation with *Batis*.

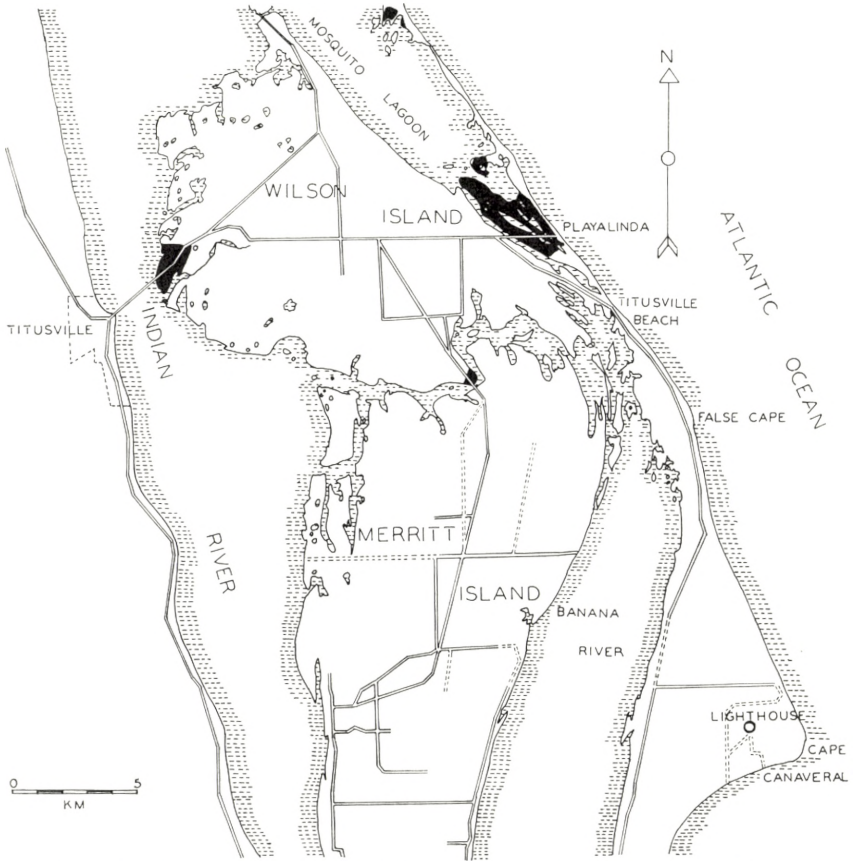


Fig. 10. Sketch map of the Titusville area on the East coast of Florida. Black markings indicate breeding areas.

In 1954 the large *Batis* marsh on the coast of the mainland at Scottsmoor was the center for a very large outbreak.

Observations on migrations indicated a breeding area on Canaveral Island which we crossed only once. At that time it was without roads and we did not find any breeding area. It might have been along Banana River.

#### *Cocoa and Lotus Island* (map, fig. 11)

The breeding areas in the bight of New Found Harbor were in the salt marsh, but the one Georgiana and Honeymoon Lake was remarkable because it was in a citrus grove and the food



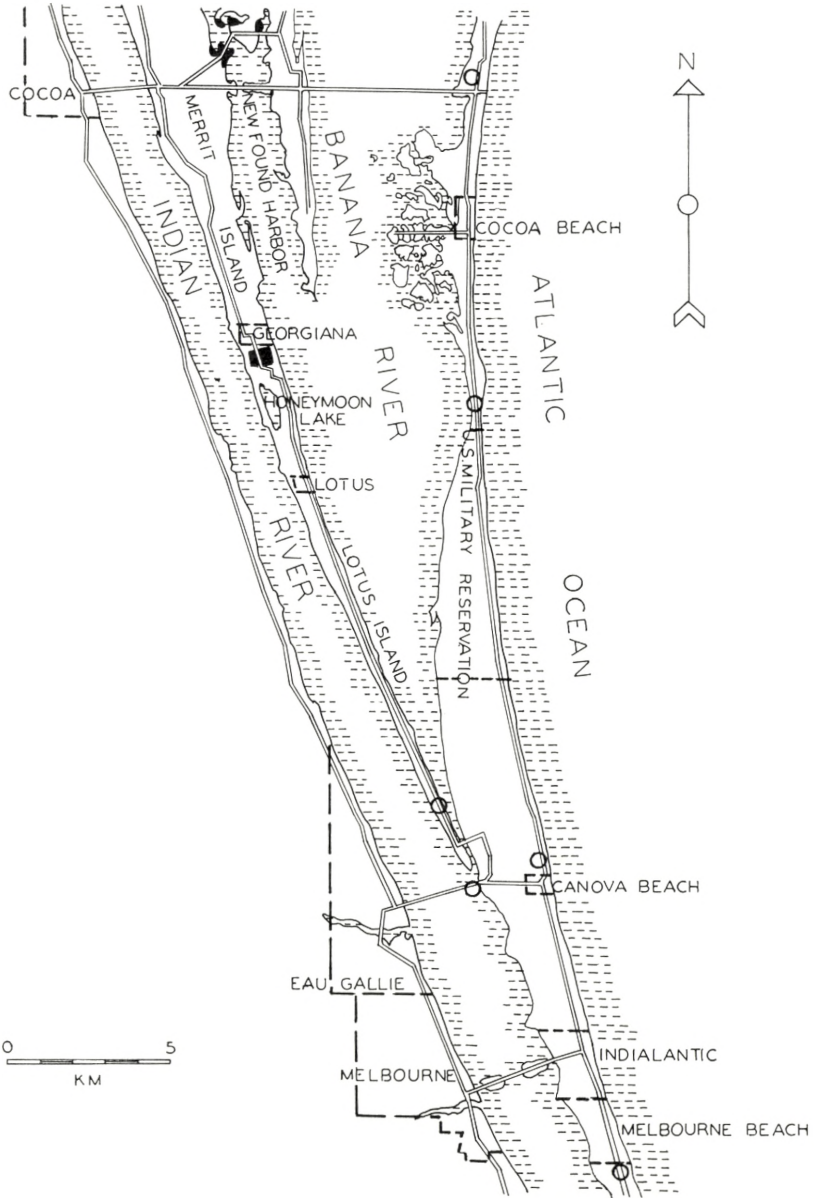


Fig. 11. Sketch map of the East coast of Florida between Cocoa and Melbourne. Black markings indicate breeding areas, circles, the main places for observations of migrants.

plant was *Lepidium*. The population was much larger than in the small inland populations with the same food plant.

#### *Grant and Wabasso*

Observations of migrations indicated an outbreak center 15–25 km south of Melbourne. But the season was over before it was found that there were potential breeding areas on the islands in Indian River off Grant. Local people were well aware of large numbers of white butterflies which at certain times of the year came to the beach from these islands. This was confirmed by later observations.

Breeding was observed on many of the islands farther south around Wabasso; migrations originating here were observed in 1954 and 1957.

#### *Vero Beach and Fort Pierce* (map, fig. 12)

There was a breeding area on the mainland at Crawford Point, North of Oslo Road which was found after observing migrations. This area later became very well known to us after the Entomological Research Center was built on Oslo Road, and the study field belonging to the Center partly included this area.

Our main observation areas were on the Beach between Vero Beach (Rio Mar) and Fort Pierce. Going south from Rio Mar one first passed through about eight kilometers of hammock and oak without breeding areas. Opposite Crawford Point were two coves and there was a large breeding area on the peninsula between them. Regular counts were made at the base of the southernmost of the coves, Floralton (fig. 12, FL). Other points where counts were made are indicated on the map as AI, AII, and AIII, each a feeding area. At DE at small road went down to the mangrove where there was a feeding area; we did not make counts here but secured butterflies for experiments. At a place 3–4 km north of Fort Pierce Inlet, Indian River sent in two long firths nearly up to the road. Between the bight of the southernmost and the ocean is a public picnic area, Pepper Park. The road continues to the inlet, where there was a good observation place for migrants crossing the inlet, but the highway branches off in a T-crossing

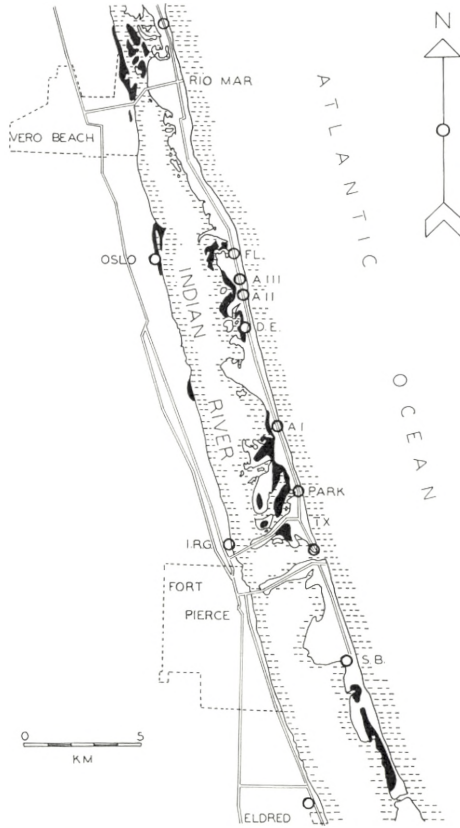


Fig. 12. Sketch map of the East coast of Florida between Vero Beach and Fort Pierce. Black markings indicate breeding areas, circles, the observations places.

(fig. 12, Tx). The road from here to the mainland was much used for observations. There was a breeding area south and east of that part of the road which we called the curve. Nearly all of these breeding areas have now been destroyed.

A little north of the bridge on the mainland we had an observation place for migrants following the coast line, at Indian River Gardens (IRG on map, fig. 12).

On the beach south of the inlet, the road ended 3.6 km from the inlet because a hurricane destroyed the road most of the remaining 21.5 km down to Jensen Beach. We had an observation site at the end of the road. There was a very large breeding area 1–5 km south of this point.

*South of Fort Pierce*

A small breeding area south of Jensen Beach was mentioned in the first report (1950, p. 5); it was not found again. Another small colony on *Batis* was once seen on State Road 703 north of Palm Beach.

At Boynton, south of West Palm Beach, the lagoon narrows down to a canal bordered by a considerable area of marsh land. *Batis* is almost the only vegetation. In February 1950 we observed an outbreak here.

**(2) Estimates of the Size of the Population**

At the beginning of this work and with less frequently visited colonies, we contented ourselves with general expressions to indicate the number of butterflies in a given population. Eventually we found that simple counting gave a fairly reliable picture of the size of the population. It was most convenient to confine ourselves to the feeding areas, and what we actually counted was not the population but that fraction of it which at the moment was feeding. The size of this fraction was unknown, even though later it was found possible for us to estimate it (see p. 31). It is certain, however, that this fraction varied with a number of different conditions: the hour of the day, the weather, the flowering of plants, the average age of the population, and probably more factors affect the proportion of a population found at the feeding area at a given moment. But even with all these limitations the method was found useful.

The accuracy of the actual count was tested by two observers (A. T. N. and E. T. N.) simultaneously walking through the area in opposite directions. We tried this five times within three days in the same area. One observer got a mean of 154, the other, 147. The single counts differed from 2 to 26, and treated as double determination, the standard error of a count was found to be 8 %. During the observation period, the counts in this area varied between 8 and 503 in the hours of activity.

In 1954, 21 more counts were made simultaneously by two observers (H. T. N. and E. T. N.). The individual counts varied from 2 to 642. The averages of the counts made by these two

persons were 104 and 94 respectively, and the error on a single count was 14 %.

On the stretch of road between the bridge and TX (see above) the counts were made by driving slowly (about 20 mph) in a car. Simultaneous counts walking and driving showed that the number found by driving was 70 % of the number observed by walking. It is obvious that some are overlooked while driving, but in walking some will also be counted more than once.

### (3) Marking: Methods and Experiments

It was clear that a method of marking the butterflies would be very useful. COCKBILL (1942) has summarized a number of methods, all, however, incorporating the disadvantage of having to catch the animals and mark them individually. The simplest of such methods is to print directly on the wing by means of a rubber stamp as proposed by Mr. C. A. ANDERSON of Dallas, Texas. We used this method for individual identification in laboratory experiments.

The ideal method for field work must be (1) fast enough to permit marking a large number of individuals in a short time, (2) gentle enough to have no effect on the behavior of the animals, (3) specific enough to permit recognition of single individuals or groups of individuals, and finally (4) distinct enough to be recognized at some distance. We have not been able to conceive a method which is satisfactory on all points. After a number of trials, the following method was adopted to mark a non-migratory population. A modification for marking migrants was later developed (see below).

A suitable dye (methyl violet, methylene blue, victoria green, or eosin) was dissolved in denatured alcohol to a concentration of 15 grams per gallon (= 3.78 liters, or about 0.5 % by weight). Such a solution was sprayed on feeding butterflies by means of an oil can; we used a "Plews Oiler", which had a capacity of 0.1 gallon (380 ml). With a little training it was possible to hit a butterfly up to a distance of 7-8 m by a few strokes of the trigger.

As to speed, this method is satisfactory. Two persons could easily mark 300 butterflies in 20 minutes, and if there had been

butterflies enough we could have marked more than 1000 per hour. One gallon of solution would mark 1000 butterflies.

How much of a butterfly is colored by this method varies; some will be totally covered, others will get a few spots. Only such markings which could be seen at a distance of 10 m were counted. If more than half the wings were colored, the butterfly could be identified in flight 30–50 m away; a totally covered individual could be recognized at almost any distance at which it was possible to see that it was a butterfly.

The vast majority of the butterflies were not much affected by the coloring. Those which were completely covered were sometimes unable to control their flight. This was especially noticeable when eosin was used. As long as this solution was wet it had a dull yellow color and the butterfly flew irregularly with the wind. After a few seconds the alcohol evaporated, the dye changed to the well-known bright pink, and the flight changed direction and became normal. Totally covered butterflies sometimes dropped to the ground but with few exceptions they recovered and flew away. The exceptions represented less than one per cent of the marked.

Besides a number of preliminary experiments, four experiments with the above-described marking method were carried out in March 1950 in the Fort Pierce area (cf. map, fig. 12).

*Experiment 1:* In the afternoon of March 7, 100–150 *Ascia* were marked with eosin. Immediately after the marking was over, about one of every four butterflies was marked. A quarter of an hour later most of the marked individuals had disappeared from the area, but during the subsequent half hour marked individuals were seen up to 150 m on either side, feeding along the road. Three days later, three marked individuals were seen feeding on *Lantana* in the marking area. Inspections after four and six days later were negative.

*Experiments 2:* This experiment was carried out at AII, a 15 m long patch of *Bidens* along the road close to one of the large breeding areas. On March 9, three persons with two oil cans marked with methyl violet every *Ascia monuste* appearing in AII from 07<sup>h</sup>00' to 11<sup>h</sup>30' and from 14<sup>h</sup>10' to 16<sup>h</sup>00'. The first butterfly arrived

at 07<sup>h</sup>25', and only five came before 08<sup>h</sup>00'. The rest of the morning about 250 were marked per hour, 991 in all. Returning in the afternoon we found hardly any marked one, and in less than two hours 930 were marked, bringing the total for the day up to 1921. The results of inspection on the following days are given as table 1, 2, and 3 and will be discussed below.

*Experiment 3:* The next marking was made in AIII, about half a mile to the north of AII. Between 07<sup>h</sup>30' and 12<sup>h</sup>00' on March 15, about 1200 *Ascia* were marked here with eosin. The same day, however, a number of trees in the surroundings started to bloom and attracted the butterflies to the extent that the usual method of counting along the roadsides became meaningless and at least could not be compared directly with the two previous experiments. The third day after the marking a large number of newly hatch individuals appeared, easily distinguishable because they were the first of the form with dark-winged females.

*Experiment 4:* It was decided to mark as many of these new butterflies as possible. On March 18 between 09<sup>h</sup>00' and 11<sup>h</sup>00' about 800 were marked with victoria green. We were unable to make inspections the following day. On the second day, the population was considerably reduced in number. In the marking area were 177 individuals of which one was green. Another green one was found 800 m to the south, and two more were seen among 166 butterflies in the previously used marking area, AII, half a mile to the south. North of AIII no marked butterflies were seen

TABLE 1.  
Total number of *Ascia* marked March 9, 1950.

Hour	Number	Hour	Number
07 <sup>h</sup> 25'—07 <sup>h</sup> 59' . . . . .	5	10 <sup>h</sup> 30'—10 <sup>h</sup> 59' . . . . .	170
08 <sup>h</sup> 00'—08 <sup>h</sup> 29' . . . . .	57	11 <sup>h</sup> 00'—11 <sup>h</sup> 29' . . . . .	195
08 <sup>h</sup> 30'—08 <sup>h</sup> 59' . . . . .	122	14 <sup>h</sup> 10'—14 <sup>h</sup> 29' . . . . .	300
09 <sup>h</sup> 00'—09 <sup>h</sup> 29' . . . . .	184	14 <sup>h</sup> 30'—14 <sup>h</sup> 59' . . . . .	290
09 <sup>h</sup> 30'—09 <sup>h</sup> 59' . . . . .	177	15 <sup>h</sup> 00'—15 <sup>h</sup> 29' . . . . .	240
10 <sup>h</sup> 00'—10 <sup>h</sup> 29' . . . . .	81	15 <sup>h</sup> 30'—15 <sup>h</sup> 50' . . . . .	100
		Total . . . . .	1921

among 238 unmarked. It is well worth mentioning that this same day was the first day during the experiments on which we observed migratory activity in this region.

#### (4) Daily Activity

The activity of *Ascia monuste* is limited to the daytime. Regardless of how many individuals are present during the day, from about two hours before sunset to one hour after sunrise, hardly a single one will be seen in the air. During this period they are resting, some at the feeding places but most of them in the breeding area. In open salt marsh (e. g., Boynton Beach), it was easy to observe the butterflies gathering and disappearing among the *Batis* plants; in the mangrove the resting animals are much more difficult to find.

Their appearance in the morning is rather independent of the temperature. In this respect it is instructive to compare the activity two mornings two days apart when the meteorological conditions were strikingly different. On March 7, 1950, during the marking at AI, the temperature rose from  $20.3^{\circ}$  at  $07^{\text{h}}00'$  to  $23.7^{\circ}$  at  $09^{\text{h}}00'$ . The relative humidity decreased during the same time from 91 % to 78 %. The wind was a light breeze from the south and there was a cloud cover in the southeast over the ocean, about 3/10 altocumulus. On this perfect morning the first butterfly was seen at  $07^{\text{h}}18'$ , but by  $08^{\text{h}}00'$  only a few single individuals had arrived. The number increased then, and from a little after  $08^{\text{h}}30'$  onwards the normal number were feeding in the area. Two days later the corresponding temperatures were  $10.7^{\circ}$  at  $07^{\text{h}}00'$  and  $14.4^{\circ}$  at  $09^{\text{h}}00'$  with relative humidities between 64 % and 60 %, 1/10 cirrus, and a fresh wind from NE up to 3.6 m/sec., (8 mph). The shivering observes expected a considerable delay in the appearance of the butterflies. The first one appeared at  $07^{\text{h}}45'$ , nearly half an hour later than the preceding day. But several were feeding between  $08^{\text{h}}00'$  and  $08^{\text{h}}29'$  and the normal number was in the area at about the same time as two days before, at  $08^{\text{h}}45'$ .

Rain and heavy dew fall delayed the appearance of the butterflies in the morning. They do not seem to become very active until the dew has evaporated.



When, during an outbreak, the number of butterflies rises rapidly from one day to another and many beautiful and apparently newly hatched individuals are seen, both sexes are found in about equal numbers everywhere. But a day or two after the peak of production, it is evident that there is considerable difference in the activity of the sexes. About 80 % of the butterflies arriving at the feeding area the first couple of hours in the morning are females. Well before noon the females return to the breeding area and then spend the afternoon laying eggs. From about 11<sup>h</sup>00' on, the males dominate the feeding places as much as the females did earlier in the afternoon. It is not known whether the males are just later in starting the day's activity, or if, perhaps more likely, they spend the early activity hours scanning the breeding areas for virgin females.

Not only do the males feed at one time of the day and the females at another, but a certain observation makes it probable that the same individual feeds at the same time each day (see below).

Regardless of sex, the number of butterflies found in a feeding area during a day remains fairly constant. On March 12, 1950, we made seven counts in AII and found that the number varied between 322 and 376 (mean: 345) between 11<sup>h</sup>00' and 15<sup>h</sup>20'. At 16<sup>h</sup>00' the number was 207 and at 16<sup>h</sup>25' feeding butterflies numbered only 66. Three days earlier, when marking took place in this area, there were somewhat fewer, and for the following calculations we shall suppose that a constant number of 300 butterflies fed during the eight hours of that day. During 5 1/2 hours, 1920 were marked. If as presumed, all visitors were marked, then 1920/5.5, or 350 butterflies arrived every hour, perhaps 2500 during the day. With a constant number of 300 present, the time each individual stayed in the feeding area was  $300/350 \times 60 = 51$  minutes.

On March 12 the average of marked individuals in the marking area AII (see Table 2) was 14 at the inspections made at 11<sup>h</sup>00', 15<sup>h</sup>00', and 15<sup>h</sup>20' whereas at 12<sup>h</sup>00' and 12<sup>h</sup>30' it was 7.5. The first three inspections were made at the same time as the markings were made but there was no marking between 11<sup>h</sup>29' and 14<sup>h</sup>10'. There was no marking after 15<sup>h</sup>50' either but the total number was lower at this time. To include inspections 6 and 7 (table 2)

TABLE 2.  
Marked *Ascia* in all three days after marking.

Inspection No.	Hour	Unmarked	Marked	Marked in % of Total
1.....	11 <sup>h</sup> 00'	360	16	4.3
2.....	12 <sup>h</sup> 00'	312	10	3.2
3.....	12 <sup>h</sup> 30'	339	5	1.5
4.....	15 <sup>h</sup> 10'	310	15	4.6
5.....	15 <sup>h</sup> 20'	340	16	4.3
6.....	16 <sup>h</sup> 00'	206	6	2.8
7.....	16 <sup>h</sup> 25'	66	3	4.6

in the calculations it is necessary to use the percentage marked of the total number of butterflies. The average of inspections 1, 4, and 5 is 4.7 % against 2.5 % for the other four inspections. The number of marked butterflies, at times when no marking took place, was thus only half the number at times when marking was going on. This seems to indicate that not only do the females feed in the morning but each individual feeds during a particular time of the day. This observation supports the view that the *Ascia* is governed by a rhythm, a view developed from the regularity with which activity begins in the morning and ends in the afternoon when the temperature is still high and the sun is shining brightly.

### (5) Longevity

In the laboratory the normal life span for females was 7–10 days and for males 5–6. The observations of marked butterflies in AII (Table 3) corroborate these figures.

The number of butterflies present at any given moment during the day the marking took place was assumed to be 300. Inspections on the subsequent days gave the following numbers of marked butterflies: 102, 76, 62, 2, and 2 (no inspections on the fourth day). The number of marked individuals on March 10 and 11 were probably only half of the true number because these observations were made at a time when no marking took place. Corrected figures for the number of marked individuals on subsequent dates will thus be: 300, 204, 152, 62, 27 (estimated) and 2. Neither in

TABLE 3.

Distribution of marked (m) and unmarked (u) *Ascia* in and around AII subsequent to the marking on March 9, 1950.

Distance from A II (km)	March 10			March 11			March 12			March 14	
	u	m	%*	u	m	%*	u	m	%*	u	m
0.....	411	49	11.9	295	25	8.5	360	16	4.4	235	0
0 —0.4 ....	605	33	5.6	534	21	3.9	875	21	2.3	1234	1
0.5—0.9 ....	353	12	3.4	902	13	1.4	2265	19	0.9		
1.0—1.4 ....	1019	6	0.5	609	0	0	714	3	0.4	2268	1
1.5—1.9 ....				870	15	1.7	905	3	0.3		
2.0—2.0 ....	426	2	0.5	1801	2	1.1					
Total.....	2814	102		5111	76		5119	62		3737	2

\* As seen from the increase in the total of unmarked butterflies on March 11, a large number of emergences took place. Thus percentages can be used only for comparison within each day and not from day to day.

this experiment nor in any other, with more than 500 observations of marked butterflies, were any *Ascia* seen more than 5 days after the marking. As all these experiments, except the last one, were made at a time when no migration took place in this region, it seems justifiable to conclude that the life duration of *Ascia monuste* in nature is the same as it is in the laboratory or perhaps a little shorter.

### (6) Diffusion

Although no migration took place during the first three marking experiments, the inspections showed clearly that butterflies ranged in the surroundings and at neighboring feeding places within a distance of a few kilometers. Information on this point can be obtained by comparing the number of marked individuals found each day following the marking inside and outside the marking area.

In Experiment 2, we know that on the day of marking all the marked butterflies were inside area AII. The next day 49 of the 102 marked ones observed (Table 3), or 48 % (25 of 76), and 26 % (16 of 62) respectively. The sequence found was thus very close to 1/1, 1/2, 1/3, and 1/4 for the first four days, which,

though most likely a coincidence, at least gives some idea of the process. The only other comparable figure is from Experiment 3 where the day after marking 12 of 29 marked individuals, or 41 %, were in the marking area (AIII).

This slow process of spreading out or mixing up with neighboring populations, which is a very different behavior from migration, had some resemblance to diffusion and it might be useful to borrow this name from Physics to denote the phenomenon.

If the simple fractions found in Experiment 2 should turn out to be at least approximately right, it can be seen that the rate of diffusion decreases during life. Compensating for the death rate, it is seen that the day after marking, half the butterflies had moved away from the area; the next day only one-third of those left had moved away; and the next day, one-fourth. The older the butterfly, the more likely it is that it will return to the usual feeding place.

### (7) Fluctuations in Size of Populations

In the first of these reports two outbreaks in the Fort Pierce area with an interval of about 35 days between them were thought to represent two successive generations. Later observations confirmed this interpretation.

In March 1950 regular counts were started and population estimates were made as described earlier in this paper.

At the feeding area west of Tx (cf. map. fig. 12 and fig. 13), there were three rather clear maxima: The first one was small (138) and came during the latter part of March. The last week of April showed a very high population with a peak of 640 on the 27th. The last maximum occurred on June 1, with a population of about the same size as the maximum period in April although the highest count was only 460.

The first maximum in feeding area AI (fig. 13) was not counted but occurred on March 12, at the same time as AII's first maximum. The next population increase, in April, started at about the same time as the one in AII but did not culminate until April 29 with 319 individuals, which was estimated to be a little more than the first maximum. The last maximum in this feeding area was still higher (503) and occurred on the first of June.

At AII (fig. 14) there was a very definite maximum in the

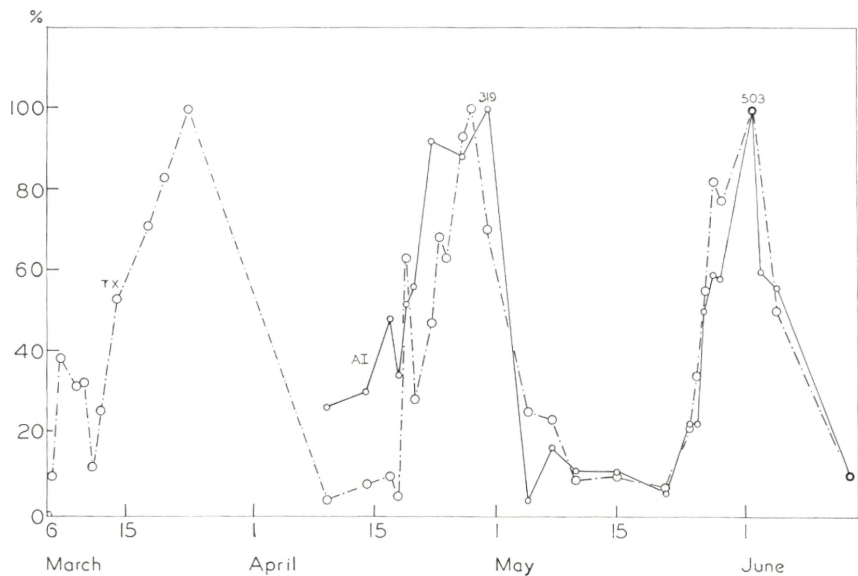


Fig. 13. Variation in the size of the population at AI (—) and at Tx (---).

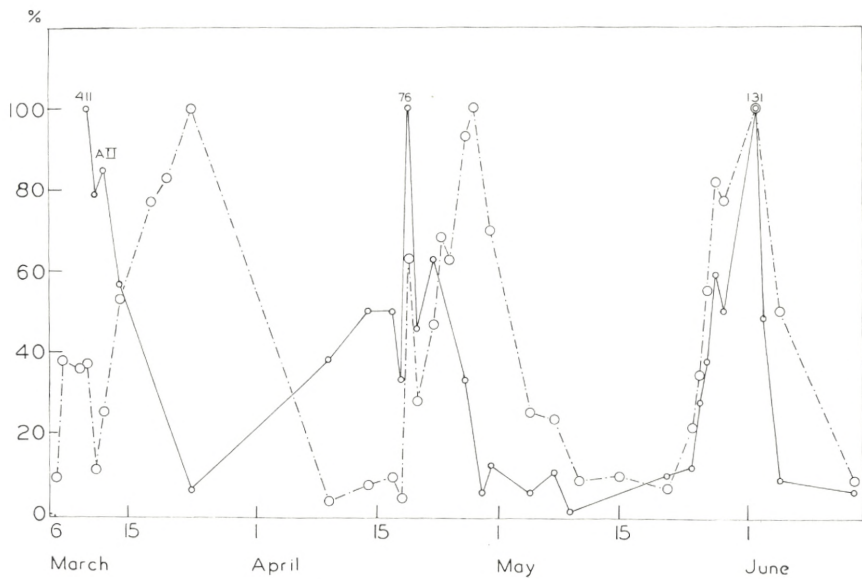


Fig. 14. Variation in the size of the population at AII (—) and at Tx (---).

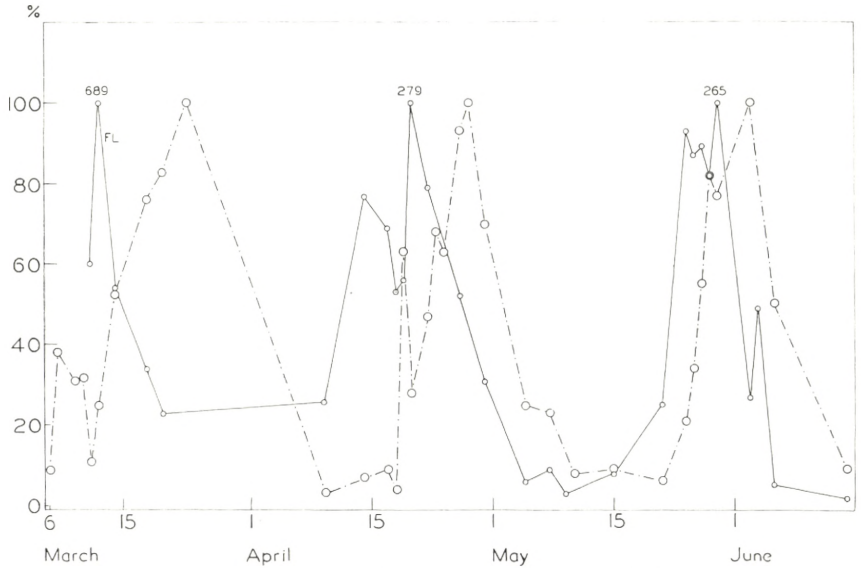


Fig. 15. Variation in the size of the population at FL (—) and at Tx (---).

middle of March, culminating on March 10 with 411 individuals—this was the second day of marking experiment 2. Later on, the population at this feeding area was rather small. There was an indistinct maximum of 76 in the latter part of April and another, somewhat clearer maximum (131) on the first of June.

At FL (fig. 15) the number increased rapidly during the early part of the month and reached the highest value counted here, 689, on March 12. There were always many butterflies in this area during the ensuing month; the lowest count was 72. On April 14 the number had again risen above 200, and the next maximum occurred on April 20 with 279 butterflies. The subsequent decrease eventually brought the number down to 8 individuals on May 9. Two weeks later it was up to 247 and remained over 200 the rest of May with a maximum of 265 on the 28th. At the last count on June 13, the FL population was down to 4.

It is not possible to present a clear interpretation of these fluctuations but a possible explanation can be advanced, as follows: In March the populations in the three northern areas (FI, AII, AI) had outbreaks in the middle of the month which were the year's highest population levels; later outbreaks were

successively smaller. The population at Tx, however, had its outbreak two weeks later in March and was just then started on its annual upsurge. Migrants from this Tx population (and from the probably simultaneous outbreak on the South Beach) settled down, most of them in AI, fewer in AII, and very few in FI. The descendants of these migrants appeared simultaneously with the generations in Tx and thus delayed the following maxima in the northern areas. In AI the maximum synchronized with Tx as early as April, in AII this happened only in the next generation, and in FI the maximum was also delayed but was a few days short of complete synchrony with Tx (May 28 vs. June 1).

In 1954 the picture was still more complicated; the populations everywhere were at a much higher level, and migrants from distant places as Scottsmoor arrived in such numbers that they obscured the regular fluctuations. It is, however, characteristic that the maximum outbreak at Tx on Fort Pierce's North Beach, which is the best observed area, occurred in 1949 on April 15–23, in 1950 on April 23–26, and in 1954 on April 23–27. In other years, especially 1957, high activity was observed during the last half of April, although the observations were too casual to determine exact dates for the maximum outbreak.

Similar regularity was found in the northern areas around Vero Beach where the activity increased towards the end of the year, and then, through one or two later waves, built up to a maximum in March after which the population began to decrease, one or two months before the population at Tx decreased.

A fact which throws some doubt on the interpretation of these observations is that the time difference between the maxima is nearly the same; at Tx in 1950 the difference between the first and second maximum is 35 days; between the second and third, 33 days. As the temperature difference between the two periods is considerable, a much large difference in duration was to be expected. An average of maximum and minimum temperatures from the U. S. Weather Bureau station in Fort Pierce was the only available meteorological data for the two periods, this average was  $20^{\circ}1$  and  $24^{\circ}9$ , resp. If the duration of the egg stage is used as an index for the effect of temperature on development, the relative duration at  $20^{\circ}$  and  $25^{\circ}$  is as 17:10 (fig. 3); in other words, if the first period was 35 days, the second should only have been

20 days; and if the second was 33 days, the first should have been 56 days. Even if this calculation is based on inadequate figures, there can be no doubt that the temperature difference between the two periods makes it difficult to understand the nearly equal periods between the maxima.

Population changes of a different kind were observed some 140 kilometers to the north of the above areas in the Titusville region. That area was inspected for some months when on December 4, 1949, an outbreak was observed. The number of butterflies increased at each following visit: Dec. 8, Dec. 31, Jan. 6, and Jan. 20. On the latter date, the numbers reached a maximum and there were clouds of butterflies not only in the study areas but everywhere on Wilson Island and even on Merritt Island. On subsequent visits, Feb. 4, Feb. 12, Mar. 25–26, Apr. 13, and May 2, the numbers gradually decreased. On the last visit only 12 individuals were seen in the enormous area at Playalinda.

These observations in the Titusville region are hardly consistent with the fluctuations in numbers corresponding to generations so characteristic of the populations in the Fort Pierce area and also in the populations at Oslo, Jensen Beach, and Boynton Beach. It is likely that they also took place in the colonies at Boca Chica and the southern Florida Keys and at Everglades City and Punta Gorda on the lower Gulf of Mexico coast although these places have been observed too little to permit a definite statement. Continuous breeding, or more precisely, breeding without synchronized generations, was not found in any other coastal population than that at Titusville, with the possible exception of Lotus Island. The latter had *Lepidium* as food plant for the larvae and thus had another point of similarity with inland populations where continuous breeding is normal.

All our observations indicate that the populations have a yearly cycle.

The unusually cold winter, 1950–1951, destroyed all the inland colonies we knew, and the coastal populations were so reduced that the numbers in 1951 and 1952 were much lower than in the preceding years. It was not until 1953 that we again saw clouds of *Ascia* at the old places, as in 1949 and 1950. We were not able to make any real observations during the following years, but what we saw confirmed our conclusions that outbreaks, migrations,



etc. occur every year at practically the same time of the year, albeit at very different intensities. In January and February 1960, Playalinda and Boynton Beach were inspected and the populations were at the same stages as in 1950. The yearly cycle consists of a passive period of about eight months during which very few of these butterflies are seen, followed by an active period of four months with greatly increased breeding occurring either continuously with non-synchronized generations or in outbreaks corresponding to three generations.

Perhaps the greatest difficulty in understanding the fluctuation of *Ascia* populations is the fact that although the cycle in any given population is 12 months, the active period (with outbreaks) is not limited everywhere to the same season. On the contrary, four of the populations studied in 1949–1950 were so dispersed chronologically that on any given day at least one of them was active: (1) The Titusville population from December to April; (2) The Fort Pierce populations from March to June; (3) The colony at Bradenton was at a maximum in August and ended in September, it had probably started its active period in June; and (4) the Punta Gorda population was active probably in August and in any case was so until November.

The reason for the sudden decrease which marks the end of the active period is another unsolved problem. RICHARDS (1940) found the factors controlling the abundance of *Pieris rapae* to be parasites which kill 75 % of the animals and predators which kill the rest. A chalcid wasp, probably *Pteromalus puparum*, was often found in the pupal cases of *Ascia*, especially towards the end of the activity periods (Titusville in February, Boynton Beach in March). A tachinid fly was also repeatedly found in the pupae. But neither these parasites nor any of the known predators (see p. 17) was the decisive factor. Many times we have marked eggs deposited on small isolated food plants and later were unable to find the newly hatched larvae, especially in the last generation of an outbreak period. They seemed simply to disappear. An unknown predator or parasite was undoubtedly at work here and probably is the most important factor in terminating the active period. It is probably a very specific enemy which after a few generations of mass production of *Ascia* propagates to such an extent that the population is reduced to the passive level from

which it takes eight months or probably six generations to return to the active stages. This hypothesis may be correct, but it still leaves unsolved the problem of why this process should take exactly 12 months.

In June 1954, we found one coccinellid larvae which sucked out the eggs. This may be the suspected predator although we have since spent much time trying to find more of them without success.

## IV. The Migrations

### (1) Definition of Migration

In order to define the term migration it is useful first to establish the term "home range" to describe the space within which a butterfly is able to consummate all the normal functions necessary to preserving the individual and the species: feeding, mating, resting, etc.

In this paper the term migration is used to indicate such a



Fig. 16. Migratory flight of *Ascia* at Narrow Point (see fig. 23). The view is toward the West across Indian River; the flight is toward the North, from left to right.



Fig. 17. Migratory flight of *Ascia* at Turtle Corner.



Fig. 18. Migrating *Ascia* on the Beach road A1A near the place where the marking took place in 1954 and 1957. A new, much wider road has now been built and only a few rudiments of the old road are left.

particular flight of butterflies by which they actively leave their home range and venture out into places which do not necessarily provide possibilities for the consummation of any of the basic reflexes known to us.

The flight of a migrating butterfly differs so much from other types of flight that even a casual observer is able to identify a migrant. The characteristics of the migratory flight, as it appears to the observer, and some of the conditions prevailing and presumably necessary for the habit of migration of *Ascia*, follow.

## (2) Appearance of the Migratory Flight

### (a) General Description

Some butterflies, e. g. the Monarch (*Danais plexippus* L.), migrate over a wide front; an observer driving from East to West will, mile after mile, cross flights of southbound individuals.

In *Ascia* the migrations occur as narrow streams in which all the individuals follow more or less closely the same track. The streams vary in width from a few meters to 10–15 meters; if the streams are wider they are usually divided into two or more streams.

Within these streams the single individuals usually fly between one and four meters above the virtual surface by which is meant the average height of the tops of dense vegetation if any. Isolated trees or bushes are by-passed by veering around them; a hedge across the flight path will cause the stream to rise over it; there are several good descriptions (FERNALD 1937 a, WILLIAMS 1930, p. 331) of "climbing" over building and several times this has been observed during the present work. In such instances some individuals will pass less than one meter above the highest point.

At the point where the migration starts, the outbreak center, there takes place what FERNALD so aptly described as an enormous milling around. During this, the butterflies often rise high in the air—up to ten or fifteen meters; also, especially in the beginning of the migration, some butterflies will still fly rather high. However, when the migratory flight is definitely adopted, the participants very rarely fly more than 3–4 meters above ground.

The migratory flight is somewhat influenced by the wind (fig.

19). Cross-winds cause the streams to form on the sheltered side of vegetation. Offshore winds cause flight along the ocean beach to be on the sea side, and, if the wind is from the sea, on the inland side behind the dunes. In calm weather the flight is often right over the top of the dunes.

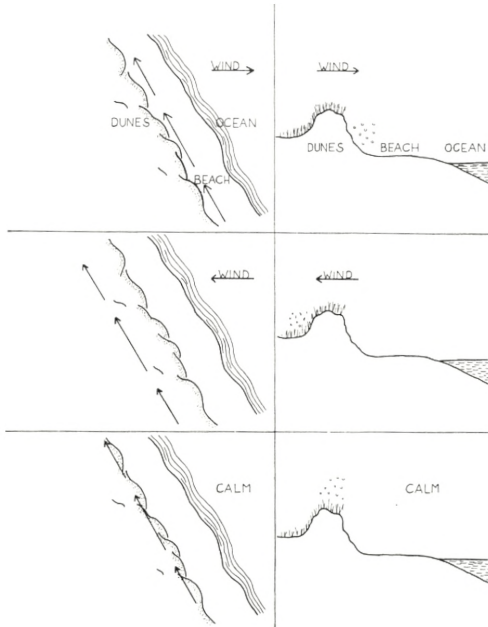


Fig. 19. Displacement of migratory flight of *Ascia* by strong winds. The figures to the left are diagrammatic maps on which the flight is indicated by arrows. To the right is shown a cross section of the same situation as shown to the left, the position of the butterflies being indicated by dots.

Strong wind, especially headwind, will reduce the height of the flight.

#### (b) Orientation

The direction of the flight is typically a straightlined course. Most of the outbreak centers on the east coast of Florida are on the long narrow islands paralleling the coast and the streams usually following the islands. When the migrations come to a wider part of an island they may branch out into several streams, but at narrow places they will unite again. On the lee side some of them may make a short-cut over a cove (fig. 20).

It was mentioned in the first report that streams often follow

such topographical features as roads, etc. ; if such a guideline makes a turn, the butterflies usually follow it if the deviation is small.

There used to be a place between Vero Beach and Wabasso where this was clearly demonstrated (fig. 21). Telephone lines on poles ran along the Beach Road and at a certain point the road made at  $20^\circ$  turn to the east while the lines continued the direction.

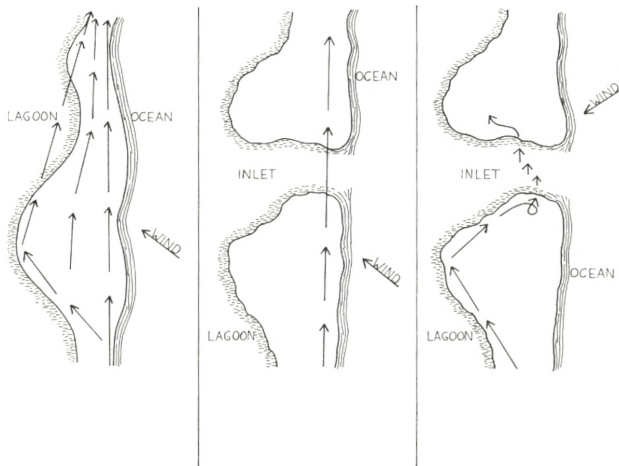


Fig. 20. Effect of strong wind on the flight of *Ascia* as indicated by the arrows. To the left is shown how a stream may be divided into 3 one of which passes over the water on the lee side.

Center figure: Flying with the wind an inlet is crossed without change of direction. Against the wind (figure to the right) the flight is modified.

The vegetation was partly removed around the lines but the cut-out was, of course, less prominent to the human eye than the paved road. The northbound stream of migrating butterflies would divide into two at this point; usually about two-thirds followed the road, one-third kept going along the lines. As a rule there was no indecision in the flight; actually, when the butterflies were 30–50 m from the turning point we could tell which ones were going to make the turn and which would keep the straight course.

The most essential modification of a flight occurs when the track leads the animals over an open place such as water or a flat, sandy area probably because of the influence of increased wind (especially headwinds) in such a place (fig. 20).

As to the orientation when crossing water the following observation is rather enlightening.

A southbound migration took place (April 3, 1950) on the very narrow Lotus Island; at the tip it crossed over to the beach island just north of the old bridge to Eau Gallie. A straight line between this point and the tip of Lotus Island is about 500 m (fig. 22).

The course of a straightlined flight from Lotus Island would be  $155^\circ$  magnetic bearing (SSE), but the butterflies did not arrive

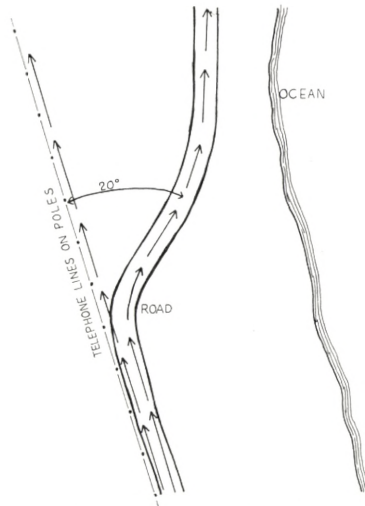


Fig. 21. Effect of topographical features on the direction of the migratory flight of *Ascia*. See text 44.

on this course—they came from the northwest or west; it was possible by means of strong field glasses to follow a single individual from the time it left Lotus Island until it arrived, and it was clearly seen to make a large turn out towards the west before it arrived. The wind was from the east, averaging 2.7 m/sec. This peculiar flight was not understood when the observation was made but a sketch map was drawn on the spot. Later it was found that this sketch corresponded exactly to one of the situations discussed by ACWORTH (1929) for an animal flying over open water in a cross-wind. There are three possibilities: (1) the animal can take account of the drift, and set the course so that the track becomes a straight line between the point of departure and the goal; (2) it can fly on a fixed course, without the ability to correct for the drift, in which case the track will be a straight line diverging from the course; or (3) finally, if the animal steadily heads towards

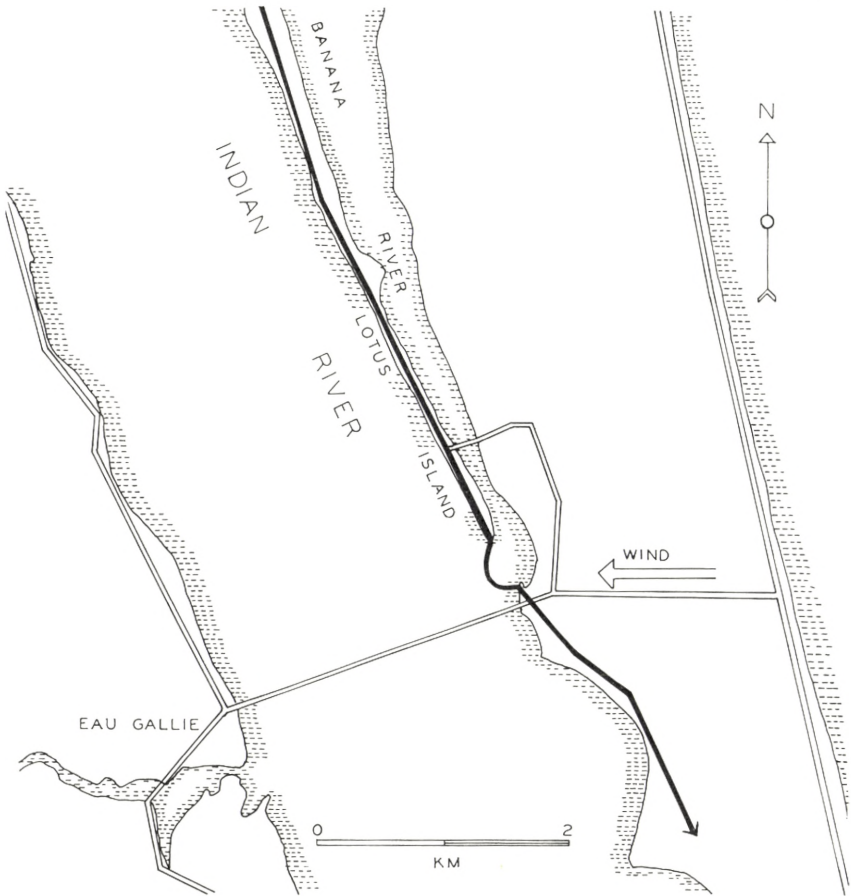


Fig. 22. Flight over open water in crosswind (see text).

the goal, but cannot correct for the drift, the result will be a curved track, exactly as sketched during the observation.

The observations on which this report is based were mostly made along the coast where the most frequent courses follow topographical characteristics; in the first report (NIELSEN and NIELSEN, 1950) examples of the occurrence of flight with fixed courses, especially in cross-country flights, were given. At that time it was unknown how the butterflies could keep their course by sun compass reaction when the sun changes position; however, after it was shown (KRAMER, 1950) that birds and insects are able to correct for the change of the position of the sun, there is no problem of understanding that the same may be the case for *Ascia*.



Nevertheless, it is remarkable that the butterflies are able to resume the same course after a night's rest as observations seem to indicate (NIELSEN and NIELSEN, 1950, p. 15–16).

Although it is obvious that guide lines and visible points are important for orientation during the migratory flight, it must be remembered that they are used only if they are close to the fixed course; in other words, the flight direction is primarily fixed but landmarks are used to follow the course. How the course originally becomes fixed will be discussed on page 68.

### (c) *Speed*

In the first part of the work (NIELSEN and NIELSEN, 1950) some consideration was given to the speed of the flight. The speed of a flying animal may be determined either in relation to the surrounding air masses (air speed) or in relation to fixed points on the ground. In estimates of the energy output produced by the butterfly, it is necessary to compute the airspeed, which can be done if the ground speed and the course of the animal is known and the direction and velocity of the wind is measured. As the butterflies have the tendency, mentioned above, to fly in the shelter of irregular objects it is very difficult to measure the velocity of the air through which the butterfly is flying, and it would often be difficult to get a usable estimate of the air speed; observations have shown, however, that the ground speed is fairly constant, and for the description of migrations aimed at here it is hardly necessary to try to calculate the air speed.

In the spring of 1949 the ground speed was found to vary between 11.7 and 16.0 km/h with an average of about 13 km/hr. The larger number of later observations confirmed this, but strong wind may produce more extreme values; against a very strong wind the speed may be as low as 8 km/h; and with a strong tail wind a marked individual once flew from a little south of New Smyrna Beach to Playalinda—a distance of 39 km—in one hour and fifty minutes corresponding to 21 km/h. But as said above, these values are exceptional; 12–14 km/h is normal speed.

In the first report (NIELSEN and NIELSEN, 1950) it was strongly emphasized that the migratory flight is very persistent: the individuals do not stop for food, and no sexual activity between migrants was ever seen. This has to be modified: migrants from

the very large outbreaks in 1954 continued the flight much longer (8–10 hours) than those in the earlier observations which lasted only 2–5 hours; those on the long migrations stopped to feed occasionally. These stops were usually very hurried and quite different from the normal flitting around; they occurred after only one or two hours flight, while butterflies on shorter migrations continued the total flight without feeding.

(d) *Dilution*

The participants in a migration seemed to move approximately at the same speed but closer examination showed that some displacements took place.

During the marking experiments in 1954 it was noted that few of the marked migrants were observed even a short distance away from the point of marking, and this was presumed to be caused by displacement.

The experiments in 1957 were meant to throw some light on this problem.

In order to make clear what is here called dilution in migration, let us consider a migratory stream of e. g. 100 individuals per minute. If for 10 minutes every individual passing a certain point were marked we would start out with 1000 marked individuals in a compact section of a stream.

Due to small irregularities in the flight the marked and unmarked individuals will begin to mix with one another. Sometime after the marking, the passage of migrants might require 20 minutes to pass a given point. At this time half the migrants might be marked, half unmarked. Later, the migrants might require one hundred minutes to pass and only 10 % might be marked. The dilution here would be expressed as 50 % and 10 % respectively.

The marking experiments in 1957 were made in order to find a relation between the dilution and the distance covered by the migration. It was decided beforehand to use the duration of the passage as an expression instead of the percentage of marked individuals in the stream; it would be easier for the observers to have to count only the marked ones, and furthermore, migrants from populations passed en route might join the migration. The distribution of the migrants is skew; a large number appear in a relatively short period and a few late stragglers may come hours

later. Therefore, we have not used the total duration of the passage of the passage but the time it takes half the main number of individuals to pass a certain point of the track.

The marking was made by alcoholic solutions of different dyes (see p. 27). The use of methylviolet was discontinued because at a distance the color could not always easily be distinguished from the dark females. Rhodamine and eosin were the most useful colors. Improvement in the technique was achieved when the fluid was dispensed under high pressure through a regular spray nozzle.

A truck with the equipment was parked at a suitable place where previous observations had shown that a concentrated stream would pass. The colored alcohol was poured into a drum which had connections for three ordinary garden hoses. The pressure in the drum was produced by compressions of the motor by means of a valve inserted in place of one of the sparkplugs. Spraying could start when the pressure reached 30 pounds/sq. inch (2 kg/cm<sup>2</sup>). For each marking, 40 gallons (150 liters) alcohol was used, and this amount was dispensed in about 10 minutes.

The experiments were carried out on April 24 and 26. The spraying took place behind the dunes about 7.4 km north of Rio Mar. Countings were made at three points, 1.7, 6.0, and 15.0 km, resp., from the place of marking. (Fig. 23). The relatively short distances were chosen in order to obtain figures large enough for calculation. All available personnel were placed at the three counting stations; the total number of marked animals was unknown, but the spraying was limited to exactly 10 minutes and it was estimated that the counts at point 3 represented 60–70 % of the marked individuals.

Table 4 shows the agreement between the two experiments. The total numbers indicate that only a branch of the migrations was observed at the points 1.7 km and 6.0 km from the marking place. The individuals counted at point 1.7 km flew directly from the marking point, while an inland detour, made by some of the individuals counted at the other points, perhaps is reflected in the slightly lower ground speed at point 6.0 and 15.0 km.

The time it lasts for 50 % of the marked to pass the observation points appears very nearly to be a straight line function of the

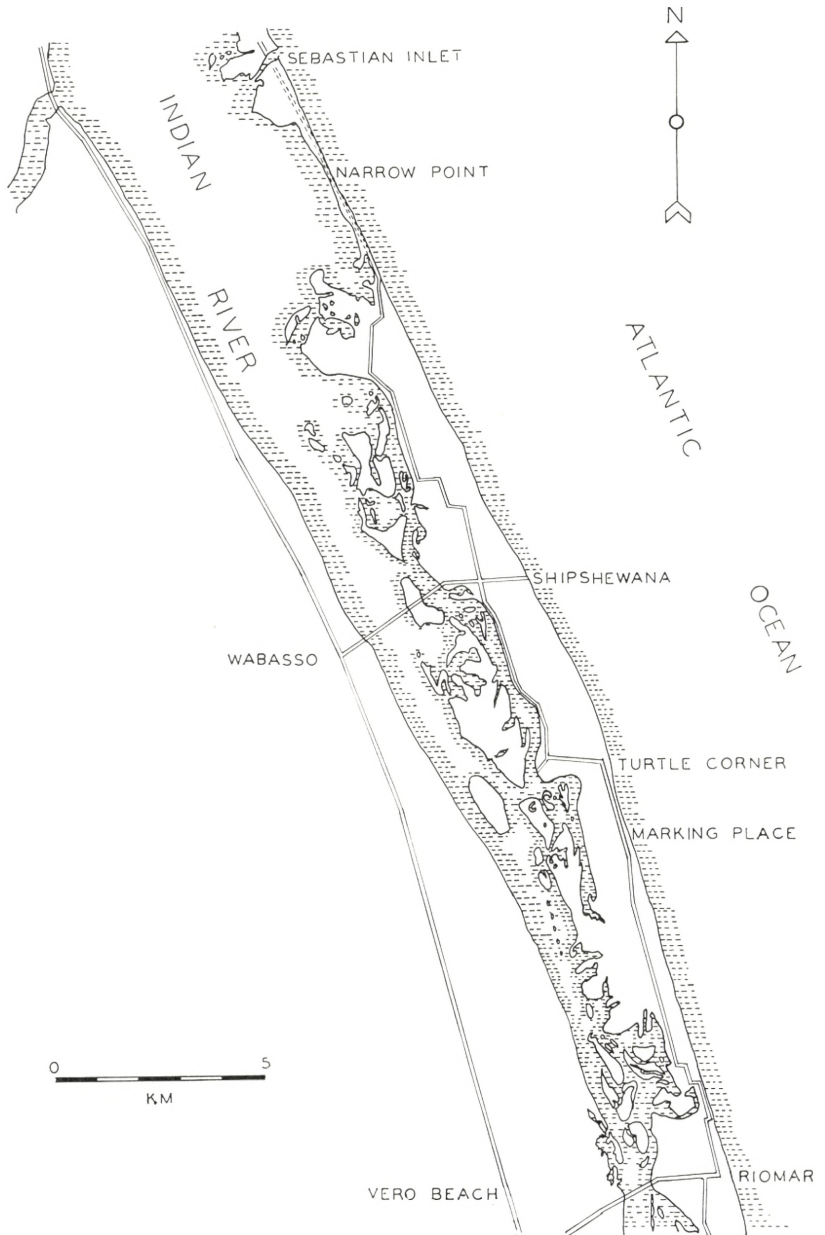


Fig. 23. Marking place and the three points of observation (Turtle Corner, Shiphewana, and Narrow Point) during the marking experiment in 1957.

TABLE 4.

Distance in km from point of marking	Total number observed		Hour when 50% were marked or had passed by		Speed of flight (km/hour)	
	I	II	I	II	I	II
0.....	—	—	10 <sup>h</sup> 06 <sup>1</sup> / <sub>2</sub> '	10 <sup>h</sup> 05'	—	—
1.7.....	83	112	10 <sup>h</sup> 15'	10 <sup>h</sup> 13'	12.0	12.8
6.0.....	42	76	10 <sup>h</sup> 40'	10 <sup>h</sup> 36'	10.8	11.6
15.0.....	225	394	11 <sup>h</sup> 27'	11 <sup>h</sup> 25'	11.2	11.3

I and II refer to the two experiments April 24 and 26 resp.

distance from the marking point (fig. 24); it has approximately the parameters

$$y = 1.00 + 0.25 x$$

and the dilution (1/y) is therefore a hyperbolic function

$$x \left( \frac{1}{y-100} \right) = 4.00.$$

The correctness of the straight line function is amazingly good which probably is incidental and should only be considered as an example of how the dilution works. We have tried to extrapolate the curve by applying it to one of the long range experiments from April 27, 1954.

About 3000 individuals were marked during 50 minutes. The main observation points were 24, 67 and 140 km from the marking point which was the same as used in 1957.

It was calculated that there should be an intensity of 9 individuals per minute at the first observation point; 112 marked individuals were observed during ten minutes which is a fairly good agreement. But at the two distant stations there were observed only 0.25 i/m instead of 3.4 i/m 67 km from the marking point; and at a distance of 140 km, 0.20 i/m were found instead of the calculated 1.7 i/m. Some of the migrants had either dropped out of the migration and stayed at one of the breeding areas passed by the flight, or a part of the migration had been diverted to another course.

## DURATION OF PASSAGE

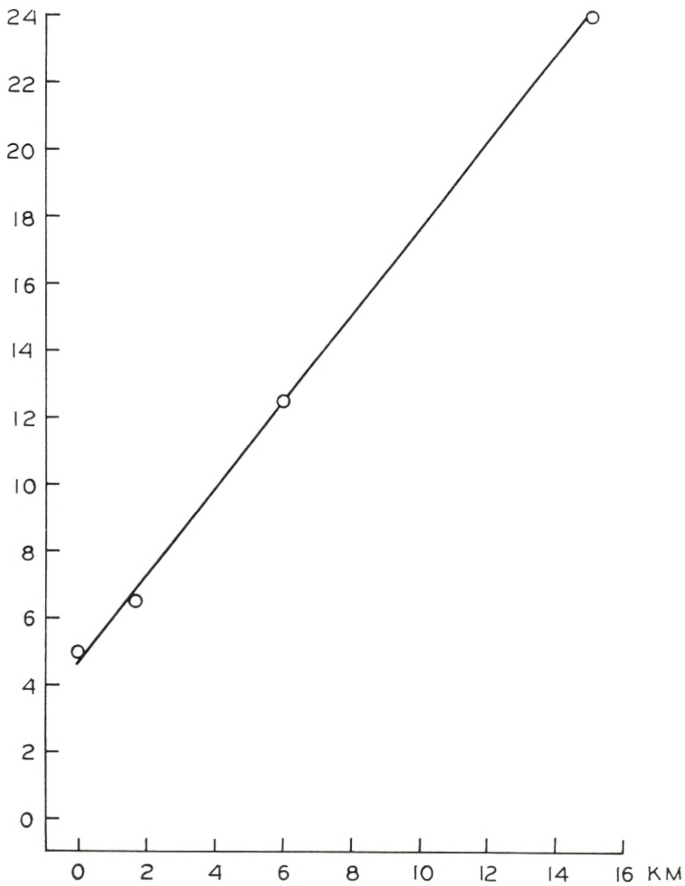


Fig. 24. Duration of the passage of the first half of a group of marked migrants as a function of the distance from the point where the marking took place.

(e) *Numbers*

The most correct expression for the number of migrants is the number per kilometer of the stream ( $S$ ), which can be calculated by counting the number passing the observer per minute ( $s$ ) and measuring the ground speed ( $g$ ) in km/hour.

We know then that:

$$S = \frac{60 s}{g}.$$

As mentioned above ( $g$ ) is normally fairly constant and no serious error is committed by using ( $s$ ) instead of ( $S$ ) if wind conditions are not extreme. During the first part of the work we found ( $s$ ) varying between 0.2 and 30 individuals per minute (i/m); HODGES (WILLIAMS, 1942) has observed migrations of 300 i/m and in 1954 we saw streams of 5000 i/m—this figure is, of course, only an estimate.

The total number of participants in a migration can be roughly estimated. As will be shown on p. 63 the number of migrants leaving an outbreak area during the first hour is about 20 times greater than during the average of the following hours; for a medium large migration lasting five hours, we might have a morning maximum of 100 i/m leaving during the first hour = 6000 individuals; in the following four hours there will be  $4 \times 5 \times 60 = 1200$  more departing, or 7200 in all.

Of course, the distance from the starting point also has to be taken into account in these calculations because the distance tends to dilute the morning maximum just as the marked individuals were diluted.

As an example a migration through Indian River Gardens originating from Oslo Road shall be mentioned; the distance is about 12 km.

The maximum density at 10<sup>h</sup> was 79 i/m; during a couple of hours around the maximum, the average was 40 i/m. If we estimate the dilution to have been 20 %, the original take-off included 12,000 individuals during the first hour and about 2400 more in the hours following. The estimated total was thus 14,400. Countings were continued that day to try to get enough figures for a direct estimate. The result was a total of about 10,000, an agreement which is sufficient considering the errors involved.

By a similar calculation the largest migrations seen, 5000 i/m, represent a total number of between a half and one million butterflies.

The casual observer of butterfly migrations might easily overestimate the number of participants. Before we learned to make a fairly justified estimate of the numbers, the striking appearance of the phenomenon gave a highly exaggerated impression.

On March 29, 1950 the southbound migration from New Smyrna Beach was observed from one of the old look-out towers

in the dunes. There was a strong offshore wind so that the butterflies flew on the lee side of the dunes on the ocean side. It looked like a white-dotted, glittering band slowly drawn along the dunes as far as the eye could see. The sight was very spectacular, and gave the impression of countless millions of migrants. Actually the average density was about 30 i/m (maximum 38) and hardly more than four to six thousand butterflies took part in the migration all day long.

(f) *Time of the Day*

It has been shown above that the activity of *Ascia* normally is limited to eight hours a day, from 08<sup>h</sup> to 16<sup>h</sup>. In 1950 the migratory activity was found to be still further limited. In the morning most of the animals fed before they took off; the feeding on flowers usually lasted about one hour. The main migrations, therefore, started normally around 09<sup>h</sup>. The end of the migratory activity was found to vary a good deal but in 1950 very few migrants were seen after 14<sup>h</sup>. The typical period of migration was five hours.

In 1954 these time limits held true for the early migrations. But as outbreaks increased in size and the density of the migratory flights were much higher than ever observed before, it was noted that the duration of the flights became longer. The migrants left the outbreak area soon after they had appeared from the resting places. It is not possible to say what the single migrant actually did, but the situation gave the impression that the urge to migrate was stronger than the urge to eat. It is hardly possible to avoid recalling the observation that migrants taking part in these large flights occasionally stopped for a hasty feeding.

TABLE 5.

Distance in km from point of marking	Duration of passage of 50 % (minutes)				Dilution
	I	II	Average	Calculated	Calculated
0.....	5	5	5	1.00	1.00
1.7.....	5	8	6 <sup>1</sup> / <sub>2</sub>	1.43	70
6.0.....	12	13	12 <sup>1</sup> / <sub>2</sub>	2.50	40
15.0.....	19	29	24	4.75	21



Without claiming that the interpretation is justified, it seems as if the butterflies in the very large outbreaks were so eager to migrate that they "forgot" to eat before taking off and later had to make up for it. Another possible explanation is that the tremendous number of animals at the outbreak centers when feeding either exhausted the nectar content of the flowers or disturbed each other so much that many of them had to leave the usual feeding grounds and seek flowers further away. The more animals there were the further they had to go and during the very large outbreaks some individuals began the migration before getting sufficient food for a prolonged flight.

The very large migrations went on until late in the afternoon, stopping first at sunset. Single individuals were even seen flying after sunset, in darkness.

It is here appropriate to mention the observations by HAYWARD (1953) of *Ascia* in Argentina; he found that the very large flights sometimes went on during the night. The differences between his observations and ours shall be discussed on p. 71.

Summarizing it can be said, that no migrations occur from the small population. From the medium-sized outbreak the migrations last from one to five hours; from the large outbreak the migrations last 8–10 hours and were continued the next day.

#### (g) *Range*

For the observers of insect migrations the question of the range of these flights has always been a point of special interest. We have in this connection first to make clear what we understand by range. First of all we have to realize that insects might be found far beyond the range carried by passive transport, e. g. car or train or a storm. But we have also observations which show that migrants which have adopted a course carrying them over areas where there is no possibility of breeding may extend the flight as is frequently the case with cross-country migrations as already observed in 1949. The normal range of dispersal by migration is the distance normally covered by an essential part of the migrants leaving an outbreak area.

To get an idea of the range of a migration by stationary observers will usually not give satisfactory results. The only two reliable methods are either to mark the individual migrants or to

follow them during the flight. In 1950 when we did not yet have a method for marking migrants, we followed the migrations by direct observation, using a car to proceed from the outbreak to the end of the flight. It was an advantage for the observer that migrations usually develop every day for several successive days, so what has been missed one day may be seen the next.

It is also helpful that the density of the departing migration is much larger during the first hour—we shall return to the reason below (p. 63).

Just outside the outbreak area the maximum passes shortly after 09<sup>h</sup> with a density about 20 times that observed later in the day. Farther away it passes at an hour which is determined by (1) the hour of the morning exodus, (2) the speed of the flight, (3) the distance from the starting point. With two of these factors known the third may be determined.

Observations at the North Bridge at Fort Pierce suggested the possibility of using this method. It was observed here that migrations toward the mainland from the breeding areas around Little Jim culminated about 09<sup>h</sup>. During the following hour the intensity decreased but at the same time an increasing stream came from the opposite direction. It appeared as if the butterflies were returning from the mainland, and for a short time this possibility was seriously considered. It was found, however, that the first flight to the mainland fanned out in a number of streams with low intensities but the eastbound stream came from a heavy flight following the coast of the mainland from north to south until it reached the bridge where part of it veered to an easterly direction.

In Indian River Gardens, 700 m north of the bridge, we found that the maximum arrived rather regularly about 10<sup>h</sup>, and it seemed likely that these migrants came from a point one hour's flight north of IRG. Most of these mornings there was a rather fresh trade wind blowing from the southeast, probably slowing the flight somewhat. Most of the coast is inaccessible but on Oslo Road 12 km north of IRG we found a good place for observation. The vast marshes here seemed a very likely breeding area, as later they were found to be.

On May 3, 1950, simultaneous countings were made on Oslo Road and in IRG (fig. 25). At Oslo the maximum occurred at

08<sup>h</sup>45' thus confirming the idea that this point was on the outskirts of the outbreak area. In IRG the maximum was observed to be at 10<sup>h</sup>13', nearly one and a half hours later, corresponding to a ground speed of 8–9 km/h. The wind was from the ESE and increased from 0.5 m/sec at 08<sup>h</sup>00' to 5.4 m/sec at 10<sup>h</sup>40'. Most of the way the migrants had a headwind of perhaps 10 km/h.

Beside the main stream there was a smaller stream over the Indian River paralleling the coast for a distance of 30–40 m. These

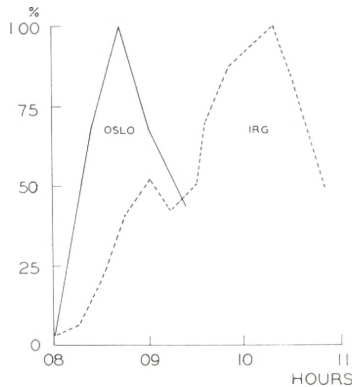


Fig. 25. Relative numbers of individuals in a migratory flight passing two points 12 kilometers apart (Oslo Road and Indian River Gardens). The numbers are given as percentages of the maximum.

butterflies were flying only 10–15 cm above the surface of the water. Eventually, when the wind rose, they came towards the coast and joined the main stream.

Some of the migrants did not turn at the bridge to the North Beach but continued south along the coast. This flight branched out again repeatedly with streams towards the beach, the last of them in the city of Fort Pierce, where they flew towards the breeding areas on the South Beach. On the coastal road going south from Fort Pierce we did not see any migration between the city limits and Eldred, a distance of about 5 km. A little north of Eldred a southbound migration was again observed but these butterflies flew in from the Indian River seemingly coming from the breeding areas around Little Jim. Simultaneous counts showed that when the maximum arrived at IRG at 09<sup>h</sup>56' it arrived at Eldred at 10<sup>h</sup>45' against a 5.5 m/sec SE wind. The distance is

about 12 km. The ground speed would thus have been 16 km/h (and the air speed well above 30 km/h) which is very unlikely. Much more likely, and in agreement with the direct observations, is that the maximum at Eldred is the morning exodus from Little Jim started at 09<sup>h</sup> and arrived at Eldred at 10<sup>h</sup>45', with a ground speed of 8 km/h.

The result of these observations is that the southbound migration from the breeding areas north of Oslo Road ended in the breeding areas at Little Jim and on the South Beach. The range was between 16 and 24 km and the duration of the individual flight between 1½ and 3 hours.

Similar observations were made on the northbound flight from the area on Fort Pierce South Beach; the southbound flights from this area were not followed closely. We found that this migration ended at All and at Porpoise Bay about 20 km north of the area and that the duration of the flight was 1½–2½ hours.

Mr. and Mrs. KARL HODGES, who for years have cooperated with Dr. C. B. WILLIAMS (WILLIAMS et al. 1942) kindly informed us in Indiatlantic near Melbourne that the southbound migrations in the spring were heaviest around noon. An examination of their notes did not show a distinct maximum but 60 % of the southbound migrants were observed between 11<sup>h</sup> and 13<sup>h</sup>. For a long time we supposed these migrations to have arrived from the Titusville area but this hypothesis met with three difficulties: (1) the migrations were not simultaneous with outbreaks in that region; (2) the distance—about 65 km—is too large to permit the morning exodus to arrive at Indiatlantic by noon; and (3) counts at the beach north of Indiatlantic showed much lower intensities than south of Melbourne Beach.

Closer examination showed that the migrations which passed through the observation area of the HODGES' came from Lotus Island (map, fig. 11); it was possible to see the migrants cross from the tip of Lotus Island as mentioned above. This flight was then traced back to the breeding areas between Georgiana and Honeymoon Lake, and to the areas ENE of the small town of Merritt Island at New Found Harbour. The distance from these areas to Indiatlantic is 24 and 35 km resp., and with normal ground speed the morning exodus could be expected to arrive at Melbourne Beach between 11<sup>h</sup> and 13<sup>h</sup>, as observed by the HODGES.

These migrations ended somewhere between Indiatlantic and Sebastian Inlet at Grant where there are islands in the lagoon with breeding grounds. The range of this migration is thus 44–45 km.

The northbound migrations usually observed later in the season by the HODGES probably had their origins in the islands. We were told by Mr. and Mrs. KARL HODGES that they usually arrived earlier in the day, before noon. This is in agreement with the shorter distance (18–20 km) from the islands to Melbourne Beach. The northbound migrations through Indiatlantic usually continued across the Cape Canaveral area to the breeding areas at Playalinda. The range of these flights were therefore probably about 65–70 km.

In spring of 1954 an attempt was made to keep track of all migrations passing the Fort Pierce–Vero Beach area. Eight migrations were clearly recognized as shown in fig. 26. The first one, (A) was small with rather few individuals, from Oslo to Fort Pierce South Beach, similar to the one observed in May 1950; the range was about 20 km. The second, (B) was a very heavy one from the large breeding areas around Scottsmoor. The southbound migration ended on the first day at Vero Beach after a flight of about 130 km; it resumed the next day, adding a distance of 25 km to Fort Pierce South Beach. The third migration, (C) was a rather small one, ranging from Floralton to Wabasso, about 20 km. Two weeks later from nearby areas at Floralton a southbound migration (D) appeared. It passed through Jensen Beach and ended probably in the marshes south of St. Lucie River Inlet at Stuart, a range of 45–50 km. It was not very heavy. The next outbreak occurred a little further south, from McConville's property close to the feeding area AI (E). It was a medium-size migration. It probably ended on the islands at Grant. A few days later followed the largest outbreak we have ever seen (F). It originated from a number of breeding areas between Fort Pierce Inlet to AI and sent equally heavy streams northward and southward. At certain points the northbound stream was estimated at 5000 individuals per minute. The first day's migration reached nearly to Playalinda, a distance of approximately 135 km. The next morning it continued for a couple of hours and added an additional 20–25 km to the range. The southbound flight against the wind went the 110 km to Boynton Beach; whether there was

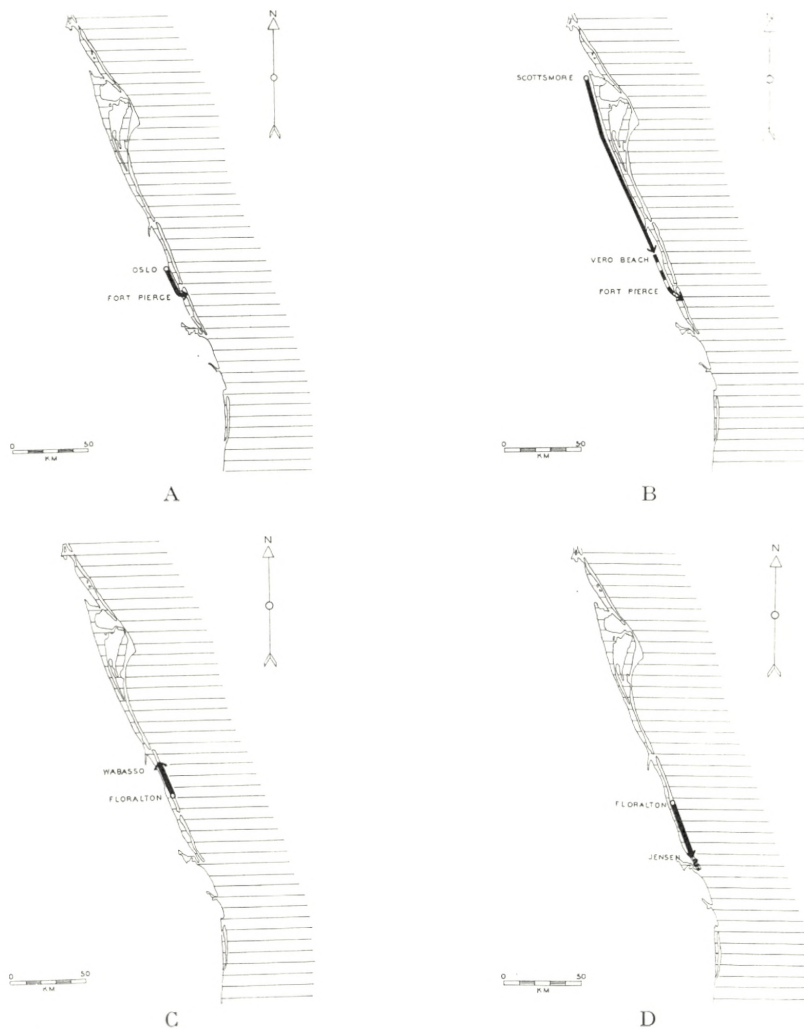


Fig. 26 A-D. Eight migrations on the East coast of Florida during the spring of 1954.

a second day's migration is unknown. The seventh migration (G) observed in 1954 went only south from Fort Pierce; it was observed at Juno Beach about 65 km from its origin but was not followed to the end. The last one (H), in June, came from the islands at Grant and went northward to Playalinda and southward to Fort Pierce South Beach.

Although these observations were rather certain it was a great relief that we were able to mark the migrants in the large north-

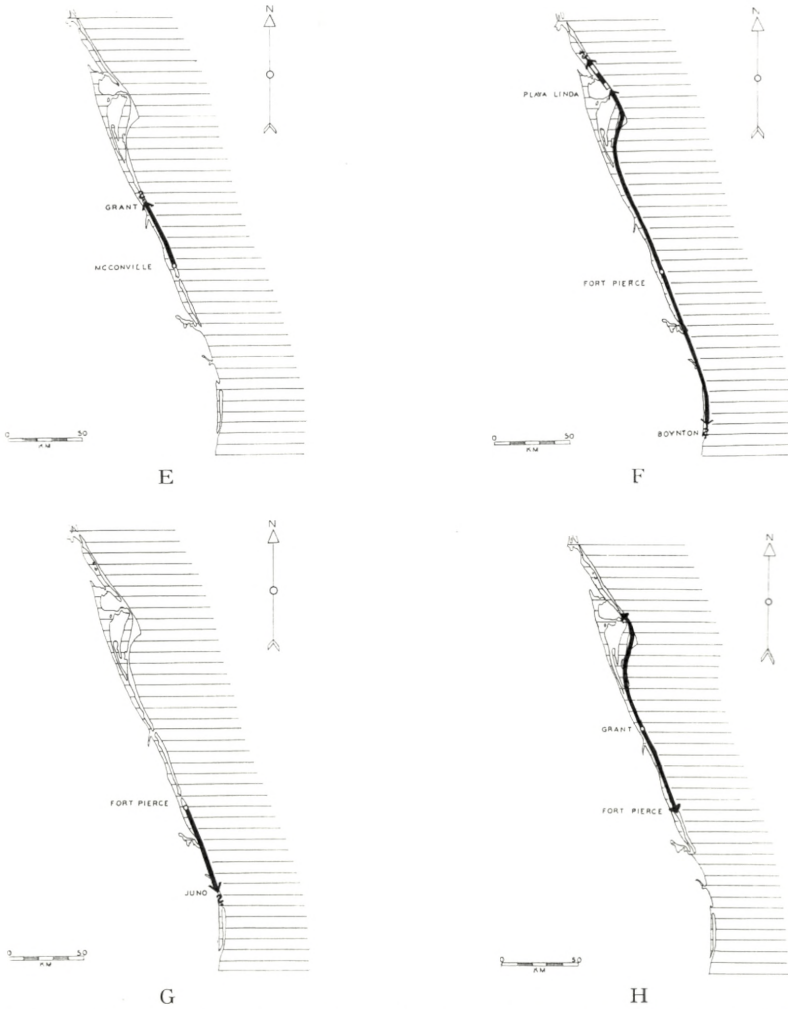


Fig. 26 E-H. Eight migrations on the East coast of Florida during the spring of 1954.

bound flight on April 27, 1954. The marking took place north of Vero Beach (fig. 23). Observations were made at several distances, and the progress followed to Cocoa Beach. The Cape Canaveral area was under military restrictions, and therefore we waited at Playalinda (see map). Calculations showed that although the animals were flying rather fast (14 km/h) with a near-tail wind from the SE, they could not be expected at Playalinda until about 18<sup>h</sup> or later. An increase in the number here indicated the

correctness of the calculation, but no marked individuals were seen.

Next morning all observers were deployed over a fairly narrow stretch of the beach about 8 km north of Playalinda. Twenty-three, perhaps 24, marked individuals were observed between 07<sup>h</sup> and 09<sup>h</sup>42' in the northbound migration. The migration decreased suddenly and stopped at 10<sup>h</sup>. The observation point was 110 km from the point where the animals were marked which again was 20–25 km north of the outbreak area.

### (3) Conditions for the Release of the Migratory Flight

#### (a) *Internal Factors*

In our present state of ignorance about the nature of migratory flight the best we can do is to describe the conditions under which the migrations start with the presumption that these conditions are necessary for the release of the migratory urge.

We have some reason to believe that this urge first appears at a certain age after emergence.

The migrating *Ascia* are always immaculate individuals, apparently newly emerged, with the wings perfectly scaled. In the sedentary populations badly rubbed specimens were often seen; they were nearly always females. As the males usually live five days and the females 8–10 (see p. 17) it seems justifiable to presume that the females become "worn" when they are older than five days.

As males and females participate in equal numbers in the migration, it seems likely that migrations take place during the first five days after emergence.

Examination of the ovaries of about 90 migrating females showed most of them were in the state of maturing; few of them were completely undeveloped, and none were completely mature. All had copulated, many of them had bursa copulatrix swollen indicating a mating less than 12 hours ago. Their age according to the ovarian development would be estimated to be 20–36 hours old. There are other ways to determine the age at which the migrations start. The following is based on observations made in



1950 when the migrations were small to medium and lasted a maximum of five hours, from 09<sup>h</sup> to 14<sup>h</sup>.

Let us presume that no butterfly starts the migration outside these hours, and furthermore, that the emergence normally is distributed over the diel as found in the laboratory with 8 % for each hour between 09<sup>h</sup> and 14<sup>h</sup>, 2–3 % during the remaining 19 hours. By finally assuming different values for the earliest age in which *Ascia* starts migrating, it is possible to calculate the relative number of individuals in each age group, and of migrants leaving the area for each hour of the diel. From these calculations it is possible to find two proportions which may be directly observed:

One is the proportion of migrants to the rest of the population; it has always been observed that some of the butterflies remain in the outbreak areas. This proportion was usually estimated to be between one third and one fifth of the population and the percentage of migrants in a population should be between 60 and 80 %.

The other proportion is made up of those leaving during the first hour in relation to the average of those leaving during the following hours. Whatever the time limits for the migration, during the night there will always be a number of individuals which have attained the age in which they are able to migrate but have to wait until morning to release the activity. In five cases countings were made all day in a short distance from a breeding area and an average found the proportion to be 19:1 = nineteen times more migrants left between 09<sup>h</sup> and 10<sup>h</sup> than during the average of the following four hours.

The effect of a number of age limits for the period of migratory activity on these two proportions has been calculated; if the limits are 10 and 30 hours, it is found that all butterflies may migrate and the morning migration would be nearly 30 times denser than the rest of the day. By trying a number of other values it is found that if the migratory period is limited to the age between 18–19 hours and 30 hours, we find that 76 % of the population will migrate, and that the morning maximum will be 20.6 times larger than the average density later in the day; both proportions thus in agreement with the observations.

On April 26, 1950, it was noted that in the morning there was

a slight increase in the number of animals (average of 388) feeding at Tx; furthermore that a few dark females appeared for the first time that year. When this place was observed again at 14<sup>h</sup>20' the number had increased to 597 and many dark females were seen. The next morning at 09<sup>h</sup>15' the number feeding had increased to 640 but there was still no sign of migration. The migration did not start until 10<sup>h</sup>30'; as the peak of emergence was about 14 the day before, the average age of the migrants at the start of migration probably was 20–21 hours.

The physiological age is probably dependent on temperature and a delay of a few hours can easily be explained by low night-temperature.

The concept of a period of delay before the migration as described here for butterflies was used to explain similar conditions in migratory mosquitoes (HAEGER, 1960; NIELSEN, 1958) and it was found to be a useful hypothesis. For mosquitoes the rotation of the hypopygium which is an indication of the physiological age of the male mosquitoes has been found to vary in duration with temperature (Dr. P. T. LUM, personal communication).

During the preceding discussion it was supposed that the eggs matured at an age of 30 hours and that the urge to migrate would cease with the maturation of the ovary. This would mean, of course, that a migration could not be resumed a second day which would be contrary to observations reported on p. 59 and 62.

This could mean, therefore, that females with eggs are able to continue migration. However, there is another possible explanation, namely the recent finding of ZÄHER and LONG (1959) that the preoviposition period in *Pieris* is longer if the larvae have been crowded.

The observations reported here do not permit conclusions to be drawn in this respect, but it seems likely that the age at which eggs mature and migration ends is higher in the crowded conditions of large outbreaks.

We have already reported some observations on the end of migrations; a specially enlightening example follows:

A branch of the migration from Oslo road to Fort Pierce on the mainland followed the railroad track through town to Orange Avenue where it turned 45° to the left, crossed the street in an acute angle, followed the house wall up to the roof, came down

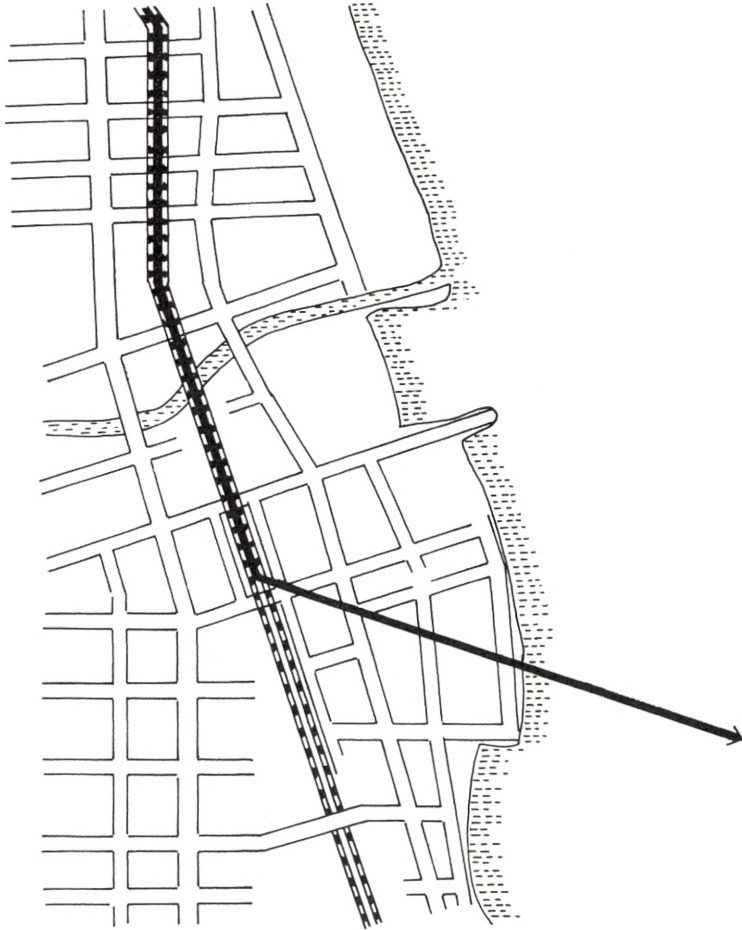


Fig. 27. The end of a migration in downtown Fort Pierce (see text).

on Second Street, and in the same way 'cut' a corner of a building three stories high on the east side of this street (fig. 27). For more than half an hour butterfly followed butterfly through these complicated maneuvers despite intervals often so long that they could not see one another.

The most likely explanation is that the salt marshes with *Batis*, which has a rather characteristic smell even for the weak human senses drew them. The wind during the observation was 5.5 m/sec from the marshes so that after the turn the butterflies flew directly against the wind.

Similar observations were made twice in 1954. In these, the wind was more to the south and the turn occurred correspondingly further north and was not as spectacular.

If the explanation is that the butterflies flew towards the smell of the breeding areas, this would imply that the migratory flight ended at the corner of Orange Avenue and the railroad track, and here became replaced by an appetential flight towards the place for the release of the reproductive behavior.

(b) *External Factors*

The external factors also play a role in the release of the migratory flight.

One of the most essential is undoubtedly the time of the day. We do not know whether this limitation of migration to a certain part of the day is dependent on an internal rhythm or on light change; it seems less likely that the temperature is a decisive factor in this respect since the beginning of the departure occurs at about the same time whenever the temperature is above a certain level.

As reported in the first of these papers (NIELSEN and NIELSEN, 1950) we found no migratory activity below  $24^{\circ}$  and nor did we observe the typical determined migratory flight at temperatures below  $27^{\circ}$ . Between  $24^{\circ}$  and  $27^{\circ}$  the flight may be uni-directional but less resolute with many stops for feeding on flowers (fig. 28).

This was generally confirmed by later observations although temperature limits were found to be more flexible. Uni-directional flights interrupted by feeding were found to be the normal means of migrating at low temperatures. We propose to call such flights "sub-migrations". The frequent remark in the reports from the HODGES, "Feeding as they fly", is a very good description of the phenomena.

The influence of temperature is clearly seen from our material gathered in 1950. Three times we have observed migratory flights at an air temperature of  $23^{\circ}$ ; they were all submigrations. At  $24^{\circ}$  five of seven flights were submigrations, and of 13 observations at  $25^{\circ}$ , five were submigrations. Above  $26^{\circ}$ , 149 flights were typical migrations.

We found no upper temperature limit for the migratory habit. Nine flights were recorded at  $30^{\circ}$  and three at  $31^{\circ}$ .

RAIN will stop migrations and prevent the start as mentioned in the first report (NIELSEN and NIELSEN, 1950). In a few cases, it was observed that a completely overcast sky without rain—a rare phenomenon in Florida—also prevents migration (e. g. March 19, 1954). This indicates strongly the existence of a compass reaction by polarized light from the blue sky as found for bees (VON FRISCH, 1950; CARTHY, 1958).

The relative humidity does not seem to have any influence on migration. Of more importance is the question of wind. KENNEDY

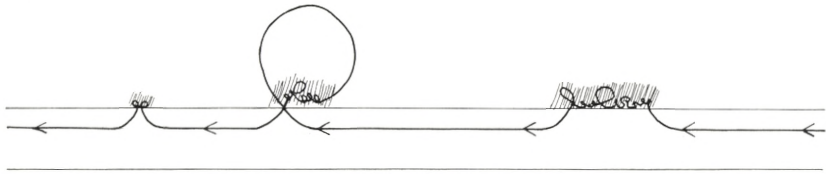


Fig. 28. Typical submigratory flight along a road. Hatched areas indicate roadside flowers.

(1957), WALOFF and RAINEY (RAINEY, 1958) have shown the role played by wind in the migratory flights of locusts. One would expect to find a similar effect on the flights of *Ascia*, but that did not appear to be the case. Except for minor changes in speed, height and unimportant displacements of the flights already reported, the wind lacks influence, particularly in the adoption of the course.

This can be especially clearly seen when neighboring populations during a simultaneous outbreak send out streams in opposite directions in the area between them. This has often been seen during this work; 70 of the 170 cases of migrations observed in 1950 were simultaneous in opposite directions. The participants usually do not pay attention to one another except when two butterflies come very close to one another. Then for a few seconds they might fly around each other as during the introduction to copulation; the flight is the same whatever the sex of the two individuals. After a few seconds they will resume their flight as before.

Although we have only seen a migrant change its flight for a few seconds after such a meeting, it is possible that at the start of a flight direction might be induced by oncoming migrants already in flight. Thus, we had the impression of migrants from

Lotus Island being "pushed" to a southbound migration by the passing of southbound migrants from New Found Harbor.

In 1954 the phenomenon was much less common. Observations of migrations were made almost daily from March 16 to June 20, sometimes at different points but in only 8–10 cases were migrations observed coming from opposite directions. The most spectacular was on April 28 north of Playalinda when a weak trickle of southbound migrants practically had to fight their way over the dunes against a very strong (second day) northbound migration.

Another evidence that wind does not play an important role in adapting flight directions is that in most cases there are simultaneous flights both to the north and to the south from an outbreak area.

If the migratory activity is limited to an age of 18–30 hours, it is obvious that departures will take place only as long as emergencies occur plus one day. In the synchronized broods of the populations in the Fort Pierce area this will occur one to three or four days in a row. In the largest outbreaks the emergencies may last more than a week, and in one case it was observed that migrations started in both directions every morning for ten days, April 19–29, 1954.

From previous descriptions of the migrations of *Ascia* one gets the impression that sometimes during the large outbreaks flights proceeded along most of the coast in the same direction. It is possible that in such cases the migrants from one population "pushed" the next one for a considerable distance, thus causing the erroneous impression of very long continued migrations.

This could also explain that the migrations in some cases have been described to go on with the same intensity all day long. If all populations between Wabasso and Fort Pierce started migrations southwards on the same morning, an observer at Fort Pierce would see one maximum after another pass: 09<sup>h</sup>00'–10<sup>h</sup>00' the local one; 09<sup>h</sup>50'–10<sup>h</sup>50' that from AI; 10<sup>h</sup>40'–12<sup>h</sup>00' from AII and Floralton. From Vero Beach the maximum would arrive between 12<sup>h</sup>00' and 13<sup>h</sup>00', and from Wabasso between 13<sup>h</sup>00' and 14<sup>h</sup>00'.

It might be asked how the original course is fixed. The answer is rather obvious to the observer. The butterflies come from their

night-time resting places to the feeding areas about which, at first, they will usually flit casually; soon, however, it will be seen that as they fly from one flower to another they continue in the same direction. The flight gradually becomes a sub-migration, a more or less straight-lined flight with stops for feeding; the stops

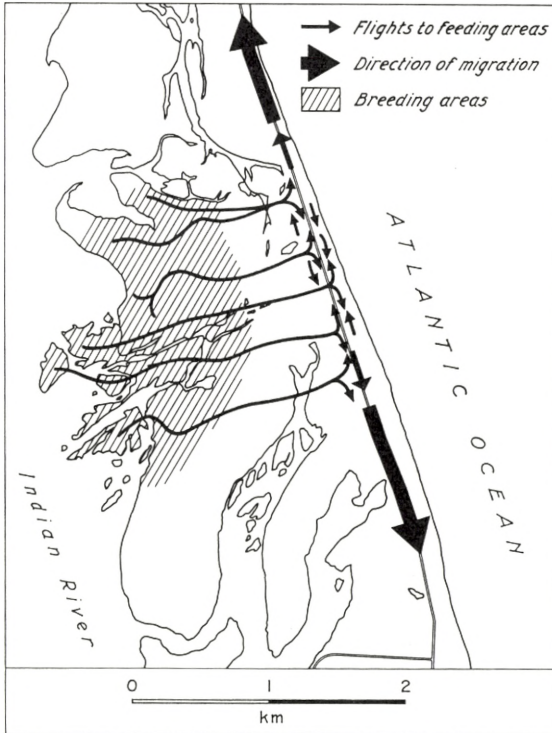


Fig. 29. Flights of *Ascia* on the offshore bar at the beginning of the migration.

for feeding become shorter with longer intervals between them until finally the migratory flight has begun. As the areas on the island where the nectar carrying plants are growing usually are parallel to the coast, the flight follows the coast line (fig. 29).

Where a feeding area has a different direction, as the east-west causeway at the bridge to Fort Pierce North Beach and at Oslo Road, the migrations usually go to the west (as the night resting places are east of the feeding area, the feeding starts in the eastern end and proceeds westward).

This is one, but probably not the only, way in which the course

becomes fixed; inter-individual influence also probably plays some role. During the milling around in the outbreak center it is sometimes seen that a flock of individuals perform flights together like a flock of birds and that they start on the migration simultaneously rather high in the air, and eventually adopt the persistent stride at the usual height. The course in such a case may be determined by a tendency to follow the course of the lower flying individuals which have fixed the course in accordance with the direction of the flight for food.

We have no observations to indicate how the course was adopted from the inland marshes. But most of the irregular flights across the interior of the peninsula can be projected back to inland breeding areas at Scottsmoor or Roseland, or east-west feeding places such as the causeway at Fort Pierce or Oslo Road.

## V. Conclusions

It will be unthinkable for a long time to come to discuss any problem of butterfly migration without referring to the work of C. B. WILLIAMS. Not only has he stimulated the interest in this problem as nobody else has, but he has elevated it from its former position as a curiosity to its present one as a major element of behavior with far-reaching consequences; he has collected an enormous number of observations and presented them in a long series of publications, three of which are milestones in this research (WILLIAMS, 1930; WILLIAMS *et al.*, 1942; WILLIAMS, 1958). In these larger publications are also found discussions of all possible viewpoints of this amazing habit.

For this work the present author wants to pay homage to Dr. WILLIAMS with a grateful acknowledgement of the inspiration he has received from him.

In this work we have tried an approach which in some respects differs considerably from that used in previous work on butterfly migration. It seemed to my wife and me, when we started this work, that to get a better insight into the nature of the migration we had (1) to concentrate on one species, (2) to familiarize ourselves with the general habits of this species, (3) to trace the migrations back to their origin and follow them to the end point,



(4) to mark the animals so that the range of flight of single individuals could be observed, (5) finally to be especially careful in observing the conditions at the outbreak centers which might be of importance for the understanding of the release of the migratory habit—a point which Dr. B. P. UVAROV brought to our attention as I am thankful to remember.

The choice of *Ascia monuste* for this work was based on the observations of Mr. and Mrs. KARL HODGES as reported by C. B. WILLIAMS (1942). The choice was extremely lucky as *Ascia* undoubtedly is one of the easiest species to investigate. The clearly defined populations, the streamlike form of the migrations, in most cases only in two directions, and the road system which usually permits the following of streams over most of their range; all these features make this species especially useful for the study as we intended to do it.

It is unavoidable that our observations in several points are in disagreement with the general concepts of C. B. WILLIAMS and his pupils. As we have concentrated on this one species we have to be careful not to make unjustified general statements; maybe *Ascia* is an exception to the general rules; but we have learned some facts about this butterfly and its migrations and if they are not in agreement with the concepts, it does not mean that the concepts are wrong but that their general validity is limited.

There is actually no reason to expect all butterflies to migrate in the same manner. HAYWARD's observations on *Ascia* in Argentina (HAYWARD, 1953) show clear differences from our observations in several respects: the migrations take place over a wide front and the migrants rise in favorable wind up to 5000 feet above the ground; and the Argentine *Ascia* sometimes continues the migration during the night.

The numbers migrating in Argentina as described by HAYWARD are much larger than those we have seen; whether this is the reason for the differences in behavior or whether the reason lies in the differences between subspecies remain to be shown. The Argentine *Ascia monuste* is the f. *automate*, the subspecies in Florida is f. *phileta*.

With these differences within one species there is all possible reason to be cautious in making general statements about migrations of butterflies from the observations of but a single one.

During this work an intense feeling was acquired of the importance of some knowledge of the general behavior of the animal for study of the migration. Most of the literature (BALL and STONE, 1928; FERNALD, 1936, 1937 a, 1937 b; JOHNSON, 1899, 1929; SCUDDER, 1889; STIRLING, 1923; and the HODGES, WILLIAMS *et al.*, 1942) deal solely with descriptions of the migrations; only FERNALD wondered about the origin of these animals.

Pertinent to the behavior of *Ascia* are only two publications: WATSON and TISSOT, 1942, state that *Ascia monuste* is "by far the most common and troublesome pest on cabbage and collard" in Florida, and give one and a half pages of description on the best way to control this "pest".

It is obvious that if we had been guided by the literature during these observations we would have had a completely erroneous picture of the origin of the flights; although during the first half year we examined every cabbage field we could find, only two larvae were ever found on cabbage.

The other publication is a paper by CHERMOCK (1946), who observed migration south of Miami; he describes how up to 500 imagines fed on an area of half an acre (by comparison, in ALL the feeding area was a strip of *Bidens* covering about 30 m<sup>2</sup>; the normal count here during the marking experiment was 300 individuals—a density corresponding to 20,000 per half acre).

Based on these observations CHERMOCK advances a complete theory for the migration of *Ascia*: An abundance of food plants for the larvae ("various Cruciferae") combined with favorable "ecological conditions" is postulated at certain times to produce a "population swarm".

In the otherwise so luxuriant subtropical flora of Southern Florida, there is certainly no abundance of cruciferous plants; and the statement seems to indicate that it is not based on observations but is a presumption based on the well-known fact that Pieride larvae in temperate zones predominantly are feeding on Cruciferae. As to the "ecological conditions" it is not specified which conditions the author has in mind; nor is there any indication of how these conditions are favorable to the animal or if they have been found to be present in the field.

CHERMOCK postulated further that when a population swarm (whatever that is) has been produced, the "environment" will

exert a "biological pressure" on the adult butterflies and they will therefore move to a more suitable environment.

Translated from the peculiar idiom of dogmatic ecology to plain English, the meaning is that if there is food enough for the larvae but not for the imagines the latter will move to a place with more food. This is just as utterly wrong as it is unfounded: (1) the migrations always originate in an area with abundant food; (2) dissection of migrants in the beginning of the flight shows that they have usually fed shortly before—anyone who has driven an automobile through a migration will remember that when migrants are killed against the windshield a big splash of more or less digested nectar drips down the glass; (3) Except in special cases of very long flights the migrants do not pay any attention to the occurrence of plants to feed on during the migration.

Any attempt to explain the migrations of *Ascia* as a search for food is wrong.

In his recent book, C. B. WILLIAMS (1958) mentions that the idea of long range migrations often are brought in doubt because of the "widespread misconception, still found in many places today" that the lifespan is too short to permit such flights.

In *Ascia* we have ample evidence that the normal lifespan of the males is about five days and of the females about ten. These figures were first determined in the laboratory and later confirmed by numerous observations in the field. In every case where we watched a population in outbreak, it was found that if no immigration occurred the number of butterflies decreased to a very low level within a couple of weeks after the maximum. The experiments with marked butterflies in a sedentary population was also in full agreement with the laboratory findings.

In *Ascia* the lifespan is short and the period during which there is an urge to migratory flights constitutes only a fraction of the lifespan—in many individuals the flight lasts only a few hours—the maximum found in this work, about one and a half days.

There are reports of butterflies laying eggs in pauses during a migration (WILLIAMS, 1958, p. 182) but they are exceptions. If our findings and conception of the end of the flight of *Ascia* is right, there will be a transition period of "moods" after the eggs have matured during which the animals will continue the migration until the reproduction "mood" is released by an external stimulus.

There are not yet enough observations to consider this a general rule, but to my knowledge there is nothing known to oppose the view. The exceptions mentioned are not quite unlikely to occur during a transition period.

Not much is known about the duration of the life of butterflies in the field; it might be worthwhile here to refer to some marking

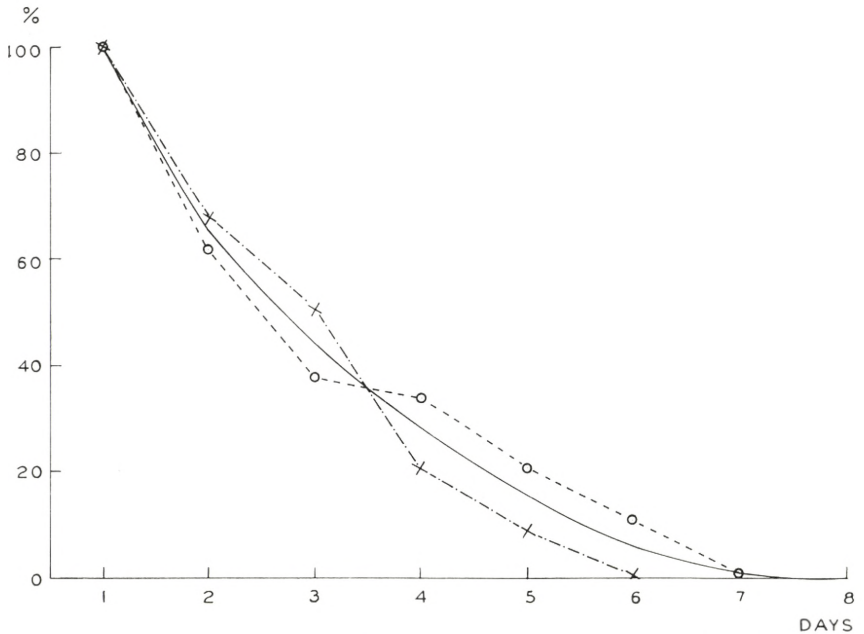


Fig. 30. Rate of disappearance of individuals in a population of British butterflies according to COGBILL (1942) (0), and in a population of *Ascia* (X).

experiments summarized by COCKBILL (WILLIAMS, 1942, p. 222–226).

During the years 1936–1939 markings were made in England of 394 *Pieridae* (*P. rapae*, and *P. brassicae*) and of 716 *Nymphalidae* of five species (*Vanessa io*, *V. urticae*, *V. atalanta*, *V. cardui*, and *V. C-album*):

To compare their findings with the countings of *Ascia*, the daily recoveries for the first seven days are given as percentages of the number found the first day. The percentages used for *Ascia* are from the figures for marking experiment II during which no migration took place.

The result is given as fig. 30. It will be seen that there is no definite difference. During the first days the English butterflies seemed to decrease faster than *Ascia*; whether this was due to an emigration, as presumed by COCKBILL, is a question, but it is a possibility; the last day the decrease was slower than found in *Ascia* which also could be expected; even if the two groups had the same death rate under identical conditions, the British individuals would undoubtedly have a longer life span in the cool summer in England compared with the March temperature of Florida, even if the difference is not very great.

After these introductory remarks the main problems of the migrations of *Ascia monuste* can be discussed.

The first of these problems (A) *Why do Ascia migrate?* actually consists of two questions:

**(A I) What is the Biological Significance of the Migration?**

The answer seems obvious: As the populations are very unstable it is an extremely useful habit that in periods of a large outbreak the majority emigrates to other potential breeding areas so that in periods of minimum size the original populations may be repopulated.

This explanation is simple and in agreement with the observations. It is presented here as a mere possibility for those who want a teleological explanation.

The author must confess to be rather uninterested in efforts to establish causality on guesswork; even when they are seemingly very clear they might still be wrong and thus be a serious hindrance in the understanding of habits. And, in any case, they do not explain anything.

**(A II) What is it that Makes an *Ascia monuste* a Migrant?**

This question has again to be divided into two parts: What produces the urge to migrate? and What releases the migratory flight?

As to the first point there is hardly any doubt that the urge to migrate in *Ascia* is produced by crowding, and it appears only in a certain period of the life of the butterfly. Both factors need further elaboration.

When this study began we had no idea of an age limit for the migrants. It is, of course, well known that locusts stop migrating at the time of oviposition; and the same seems to be true for *Ascia*.

It is actually more difficult to understand the delay in the appearance of the migratory activity. It cannot be explained simply as a waiting for the hardening of the chitin, a process which only lasts an hour or less. In mosquitoes a similar period of inactivity was found (NIELSEN, 1958) lasting 6–8 hours. In some species the extension of the fibrillae on the antennae is a good indication of preparedness for prolonged flight (NIELSEN and NIELSEN, 1958); and the delay of this habit shows that there is no urge to prolonged flight until after the inactive period even when the stimulus to flight is present.

From the consistent result of many observations we know that migrations occur only in large populations of *Ascia*; and the migratory activity is more intense the larger the population is. From this it can only be concluded that crowding is at least one of the factors producing the migratory "mood". "Crowding" as used here means a situation in which an abnormally high number of individuals are concentrated within certain spatial limits.

The importance of crowding in the behavior and phase change of locusts was shown many years ago and a similar relationship between crowding and migration has been found in so many cases that it is reasonable to accept it as a general rule.

How the crowding produces the migratory urge is, of course, a very fundamental question—with no answer available. Pertinent to this question are observations on gregariousness in *Ascia*. The very young larvae from the same batch of eggs will sometimes stay closely together as described in the first report (NIELSEN and NIELSEN, 1950). This tendency to gregariousness is never seen in older larvae, and the pupae are always found far apart.

If the stimulus for the migratory urge is derived from contact between individuals—and the effect cannot very well be understood otherwise—it is most likely that it occurs after the emergence when the butterflies are incessantly meeting other individuals. It is also doubtful whether the density of larvae per unit of area in the small inland populations is less than in the medium-sized outbreaks in the larger colonies at the coast; but the absolute number over a vast area will be so much larger that the adults will be surrounded all the time by other individuals wherever they

move, especially at the places for feeding and at the night resting places. However, in the experiments mentioned (p. 14) to show a delay in sexual development by crowding, the only possible delay was found in crowding the larvae.

If it is true that the stimulation to migrate is produced by contact of the butterflies after emergence it seems not unreasonable to consider the 18-hour period before the urge appears as one during which the effect of the stimulus accumulates a sufficient "motivation" to permit the adequate stimulus to initiate the actual flight.

In mosquitoes the situation is different because the immature stages have a strong tendency to aggregate; maybe this is the reason why the pre-migratory period in mosquitoes is so much smaller than in *Ascia* (1-2 % of the average lifespan (400 hours)) while in butterflies it is about 10 %; in *Ascia* the migration stops after 15 % of the lifespan is over and a similar figure (17 %) is likely to be case for mosquitoes although our knowledge here is definitely incomplete.

The next question (All b) is what conditions will bring *Ascia* to the consummation of the migratory urge when it is present; in plainer language; under what conditions do the migratory butterflies start the migration?

This has already been discussed (p. 62) and it should be only summarized here that the four conditions are (1) the right time of the day, (2) a suitable temperature, (3) visibility of the blue sky, and (4) absence of heavy rain.

### B. How do *Ascia* Migrate?

The immediate answer is: The migration is a persistent flight, essentially following a straight course in relation to magnetic bearing, one to three meters above the ground.

But this answer leads to a series of other questions, most of which already have been discussed (p. 42) and here need only to be mentioned.

#### BI: How is the Straight Course Adopted?

The migrations are preceded by feeding; at least in some cases the course is a continuation of the main direction of flight during the feeding. Possibly it is also guided by topographical features

such as roads and shorelines. It also seems that some individuals adopt the course by imitation of migrants already on their way.

The narrow streams formed by the migrants are typical for *Ascia*, but not for many other butterflies. The independence of external factors, especially wind, is clearly seen by the facts (1) that south of an outbreak center the migration will go southward; north of it, it will go northward, etc.; (2) that migrations frequently occur in opposite directions between two outbreak areas.

### **B2: How does the Migrant Keep the Course?**

There does not seem to be any other possible explanation than a sun-compass direction. As the migrations do not stop when the sun is momentarily hidden behind clouds it is most likely that the orientation is based on polarized light. Our observations are in agreement with this concept but they do not prove it.

Besides the compass-based fixing of the course there is also an orientation according to visual stimuli as shown by examples given above. The guide lines are used according to their usefulness in keeping the magnetic course. The goal of flight over open water is determined by the course, and the course is kept towards this point (p. 45). This clearly shows that the orientation during the flight is a combination of a fixed magnetic course and a course toward a visual goal.

### **C: What is the Range of the Migration?**

The problem of the range of migration is not only a question of distance covered by the migratory flight, it is closely connected with the speed and the duration of the flight.

The ground speed is about 12 km/hour but varies with the wind, normally from 10–15 km/h. This variation in ground speed is much smaller than the variation in air speed. If the air speed were 12 km/h, and the wind were 10 km/h against the flight, the ground speed would be 2 km/h; and with a tail wind of the same velocity the ground speed would be 22 km/h; it is therefore, justifiable to consider the ground speed as nearly constant; it shows again that the speed is regulated by visual stimuli.

The other main factor determining the range is the duration of the migratory flight which was found to vary with the size of



the population. From the smallest population emitting migrants the flight lasts only a couple of hours and usually ends in one of the first breeding areas the migrants come to; the largest migrations last ten hours the first day and may go on for several hours the next day. Twice during this work migrations were observed lasting 12–15 hours and covering a distance of up to 160 km. The average range is a good deal shorter probably 30–60 km.

As already mentioned, it is impossible to make general statements about the migrations of butterflies from studies of one single species; yet, it is encouraging that several of the elements found for *Ascia* have also shown to be valid for mosquitoes.

The period is over when the mere recording of directional flights can be considered the central part of the study of migration. Any real progress in this field can be achieved only by an intensive study of the general behavior of the animals, of their development and of their ecological characteristics. The conditions for the production and release of the migratory habit, the longevity and the duration of the migratory urge are the basic elements on which increased insight in the nature of migration rests.

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