AMERICAN MUSEUM
NOVITATES

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CITY OF NEW YORK OCTOBER 27, 1950 NUMBER 1471

CONTRIBUTIONS TOWARDS THE KNOWLEDGE OF THE MIGRATION OF BUTTERFLIES[1]

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Acknowledgments

The observations described below are part of a research program in field physiology initiated by Dr. Laurence Irving, to whom we are very much indebted for this opportunity to carry out the work.

As southern Florida is one of the best places to study the migration of butterflies, we were fortunate in being able to use the Archbold Biological Station as a base. Our best thanks are due to Mr. Richard Archbold, director of the station, who placed the excellent facilities of this institute at our disposal, and to Mr. Leonard J. Brass, botanist, and Mr. Frank Rinald for their kind interest and help.

As we are not familiar with the systematics of Lepidoptera we are most grateful to Dr. Alexander B. Klots, who very kindly checked our collections of butterflies. We are also indebted to Dr. B. P. Uvarov for criticisms and suggestions.

So many people in southern Florida assisted us with valuable information that it is not possible here to express our thanks as we should like to do. In the following parts of the paper we shall, however, have opportunity to mention a few, as their information is included among our own observations.

INTRODUCTION

Man's knowledge concerning the ability of insects to migrate, often in large numbers and over considerable distances, dates back

[1] This work has been made possible by support of the Office of Naval Research.

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FIG. 1. Newly hatched *Ascia monuste.*

to prehistoric time. Ever since man has been dependent upon crops in such parts of the world that are exposed to the devastating migrations of locusts, he must have had some knowledge of the phenomenon, but not until the last few decades have we had any real understanding of this strange habit, even for locusts.

As for butterflies, there exists a great miscellany of observations on mass movements and unidirectional flights, and thanks especially to the never-tiring efforts of C. B. Williams all these data have been gathered together. Very few systematic observations and experiments have been made, however, to try to determine the factors governing the travels of butterflies.

From Williams (1942, pp. 142 ff.) we learned that Mr. and Mrs. Karl Hodges of Indiatlantic-by-the-Sea, near Melbourne on the

east coast of Florida, had for several years observed regularly occurring migrations of *Ascia monuste* Linnaeus, the southern white, along the coast, and we decided to concentrate on this species. Unfortunately we soon learned that very little was known about its general habits, so we had, therefore, to begin by acquiring as much data as possible on its general life history.

GEOGRAPHICAL DISTRIBUTION OF *ASCIA MONUSTE* IN FLORIDA

The initial step was to find the animals and especially their breeding areas. Holland (1947, pp. 277–279) indicates that the species occurs in several varietal forms over a vast area covering tropical and subtropical America and that it is "not uncommon in the Gulf States."

During February and March, 1949, traveling by automobile, we tried to cover as much as possible of the area in Florida south of a line from Jacksonville through Gainesville to Tampa. We found none of these butterflies in the northern part of the area, so we did not extend it farther north. In the northern part, especially west of the St. Johns River, *Ascia monuste* seemed to be substituted by *Pieris rapae*.

It may seem that motoring through the country is a rather crude method of getting information, but certain facts justified the method. First, it was the only possible way to cover the considerable area in question in the short time we had at our disposal; second, the inland populations of these butterflies are found mostly at localities close to roads; and, finally, the animals are conspicuous and easily recognized even at some distance. Closer examination was of course made whenever suitable localities were spotted and also whenever animals were seen.

The picture of the distribution we now have is as follows: the animals were abundant in a string of localities along the east coast from Key West in the south to the environs of Titusville in the north, and along the west coast from Key West northward to the Bradenton area. Inland we found several populations at scattered points: (1), northeast of Homestead; (2) at Bare Beach between Clewiston and Belle Glade; (3), just west of Clewiston; (4), south and west of Moore Haven; (5), at Fort Denaud, west of Labelle; (6), west of Brighton; (7), west of Lake Placid; (8), on Hen Scratch Road, north of Lake Placid; and (9), in Sebring.

Eventually we learned that all these localities were breeding areas and, with the exception of nos. 7 and 9, that the food plant

FIG. 2. Breeding area on Hen Scratch Road.

for the larvae was the wild peppergrass, *Lepidium virginicum*. It is well known that the pieride butterflies breed especially on cruciferous plants, and we spent a great deal of time examining cabbage fields in the hope of finding breeding areas. We succeeded only once, in locality no. 7, and even here we saw only a single butterfly and found but three nearly full grown larvae which were hatched in the laboratory to normal *Ascia monuste*.

In Sebring we found populations on nasturtium (*Tropaeolum*) in gardens during April and May; later in the year we found them on *Cleome ciliata*, a plant of the family Capparidaceae related to *Crucifera* recently introduced in Florida. *Cleome* was found on two vacant lots between gardens in Sebring.

As we learned that every time we found a number of individuals inland flying around within a limited area it meant that there was a breeding ground, it puzzled us that we were unable to find where the much larger populations along the coast were breeding. It is true that on one occasion we found a very small population on peppergrass near the beach at Cape Canaveral, but as this plant is not common in the coastal regions, it seemed doubtful that it could be the normal breeding plant. We soon realized that the distribution along the coast coincides rather well with the occurrence of mangrove, but it was not until the latter part of May that we were able to find the breeding plant. It was then found to be the saltwort, *Batis maritima* Linnaeus, which covers vast areas in

the mangrove and the salt marshes. This was first noted on the Fort Pierce Beach, about which further information is given below, and later in the year we found a population on saltwort at Gomez near Bradenton Beach.

Finally, in June and July, we found a small population at Jensen Beach where the larvae were feeding partly on a few specimens of *Lepidium* and partly on *Cakile maritima*.

Although it seems that *monuste* breeds the year round in southern Florida, the different populations seem to last only for short periods. The end of such populations may occur in different ways. The colony on Hen Scratch Road was exterminated by a chalcidian wasp (*?Pteromalus puparum*). Sometimes the food plant will disappear—*Lepidium* often dries up in late spring, and during the summer it becomes rather rare. Or man may interfere with the populations by destroying the food plants—cutting grass and *Lepidium* along the roadsides or by spraying insecticides. None of these causes for the end of breeding, however, can account for the extermination of the colonies in the mangrove; we shall refer to this point later.

LIFE HISTORY OF *ASCIA MONUSTE*

Eggs

The egg has about the same shape as a dirigible and is 1.1 to 1.3 mm. long and about 0.56 mm. in diameter at the broadest part, which is a little below the middle. The eggshell has at the top a figure very much like the stigma on a fruit, with eight to 10 lobes, from which ribs run longitudinally to the base of the egg. Generally there are a few more ribs than lobes, these ribs starting a little below the "stigma." Between the ribs the surface is very finely wrinkled.

The color is usually whitish yellow, but we have also seen greenish eggs that gave normal individuals. After approximately three to five days, depending on the temperature, the eyes of the larva can be seen through the eggshell, and on the following day the hairs, as well as the mandibles gnawing at the shell, can be seen.

The eggs are deposited upright on the leaves of the food plant. There are some differences in the way the eggs are deposited in the different populations, presumably according to the food plant. Of the peppergrass the butterflies prefer young plants without

FIG. 3. Egg on *Lepidium.*

flowers 10 to 15 cm. high. The plant is so tiny that the weight of the butterfly will bend it down. During the egg laying the butterfly will generally hold its head erect, the abdomen is directed towards one of the leaves and touches it for a moment. A few seconds later the butterfly flutters away low over or through the vegetation to find a new plant while the top of the first plant springs up to normal position with the egg on the leaf. One can easily understand why, with this procedure, the eggs are generally found on one of the upper leaves of the plant, and mostly on the upper surfaces. On *Lepidium* the eggs are deposited singly, and only in comparatively few instances were two on the same leaf; we once found three, but their main axes differed which might indicate that they had been laid at different visits, probably by different females.

On *Batis* the eggs are deposited as on *Lepidium*, and, though our knowledge is rather limited here, the same seems to be true with *Cakile*. On *Tropaeolum* and *Cleome*, however, the eggs are laid in clusters in which the number of eggs may be as high as 50. During such an egg laying the female curves the abdomen towards the surface of the leaf for a couple of seconds, then stretches it out between the wings for about 10 seconds, and then recurves it to lay another egg, and so on. Towards the end of such a deposit there may be fairly long intervals between the egg laying, until finally the animal flies away, generally to feed on some flowers.

The total number of eggs laid by a female is so far unknown, but we have had in captivity a female that produced 115 eggs in one day. We have reason to believe that a female in its lifetime is capable of laying eggs for a period of from three to six days, and the total therefore would probably be between 200 and 1000.

Larvae

The newly hatched larva is about 2 mm. long and must pass through at least four molts before it reaches the final length of about 35 mm. In nature the duration of the larval stage is about three weeks.

The full-grown larva looks very much like the larva of a common cabbage butterfly; the body is brownish green, with a yellowish stripe on each side and three greenish stripes on the back. Between the stripes each segment has four large black spots (the two on the back placed a little more craniad than the lateral ones) and several smaller spots. On the prothorax the black spots are

FIG. 4. Egg cluster and hatching larvae on a *Tropaeolum* leaf.

larger and cover most of the segment. There are, as usual, abdominal legs on the third to the sixth abdominal segments and a pair of claspers on the last. In the first instar the larva is more yellow and has fewer dark spots.

All the larvae of the egg clusters on *Cleome* and nasturtium are hatched within a few hours, and such larvae have a strong tendency to stay together. During the first two ecdyses they are very often seen in a common carpet of web, the bodies in the same direction, looking like fingers on a hand. Later they are more solitary in their habits, and when they are ready to find a place to pupate they always spread out and seem rather to avoid one another.

From the time a full-grown larva stops eating until the transformation to pupa takes place is often a couple of days. First they move about for some time seeking a suitable place. This is much easier for the animals that use the broad leaves of *Tropaeolum* on which to pupate (and the same may be true of cabbage). Caterpillars from the other food plants must find a place in the neighborhood, although in one case at Bradenton Beach

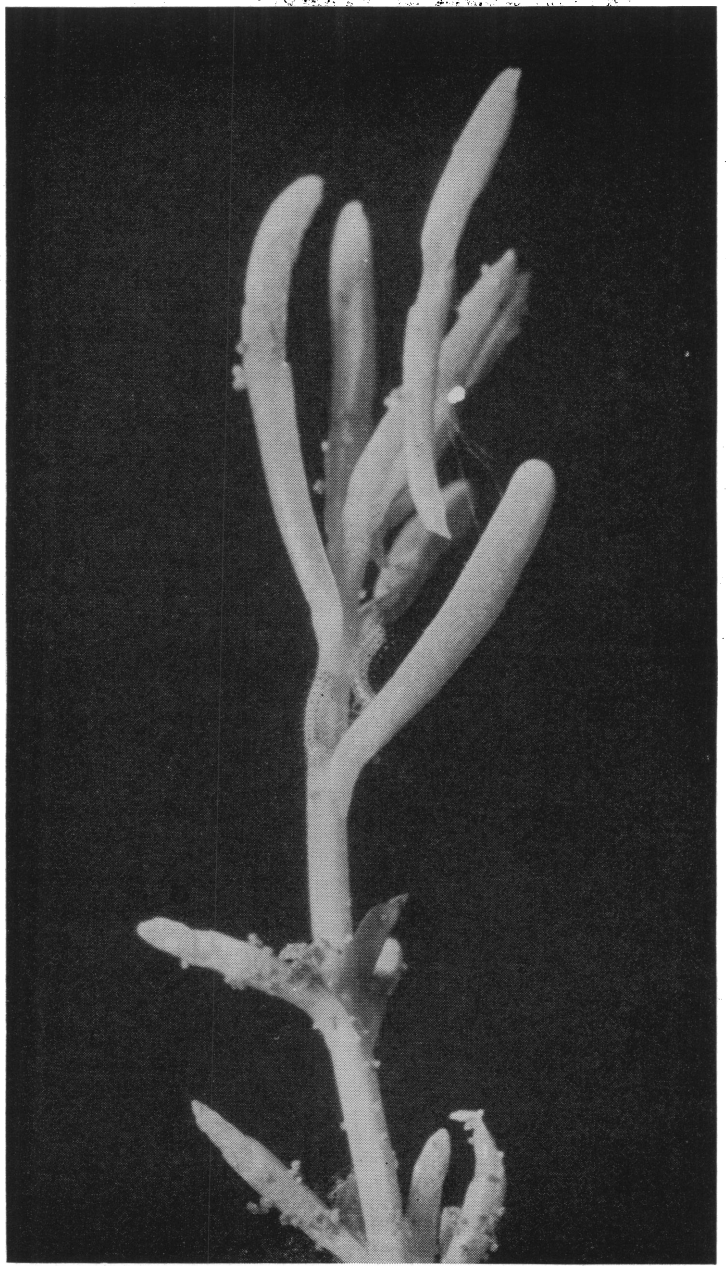

FIG. 5. Two young larvae on *Batis maritima*.

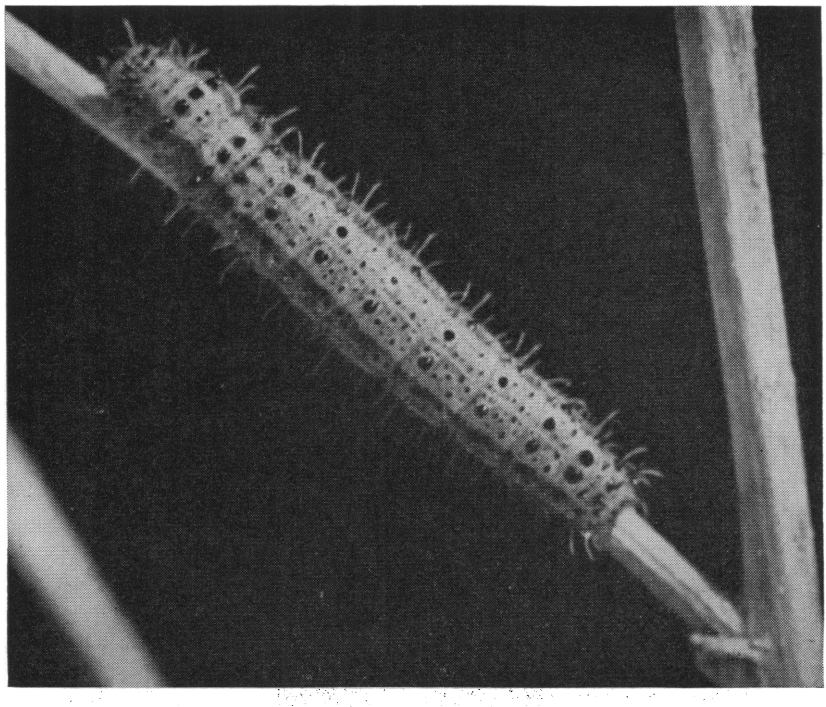

FIG. 6. Full-grown larva.

we found a pupa on *Batis*. At Fort Pierce Beach we saw a pupa on a leaf of the white mangrove, *Laguncularia racemosa;* close to the population on *Cakile* we found the pupa on the leaves of *Coccolobis uvifera*. The larvae from colonies on peppergrass generally use the stems of plants growing around them such as *Eupatorium* or *Ambrosia*. From *Cleome* we have seen them pupate on the south, exposed wall of a shed some 5 to 10 feet from the food plants.

PUPAE

When the larva has found a suitable place it spins the two webs that support the pupa. First, with the head downward, it spins a little band about the shape of the vamp of a shoe, then it turns around and places its claspers and the last segment of the abdomen in the "shoe," which soon hardens and glues the hind tip of the body to the support. By moving the head from one side to another, the caterpillar can now spin the thread that supports the

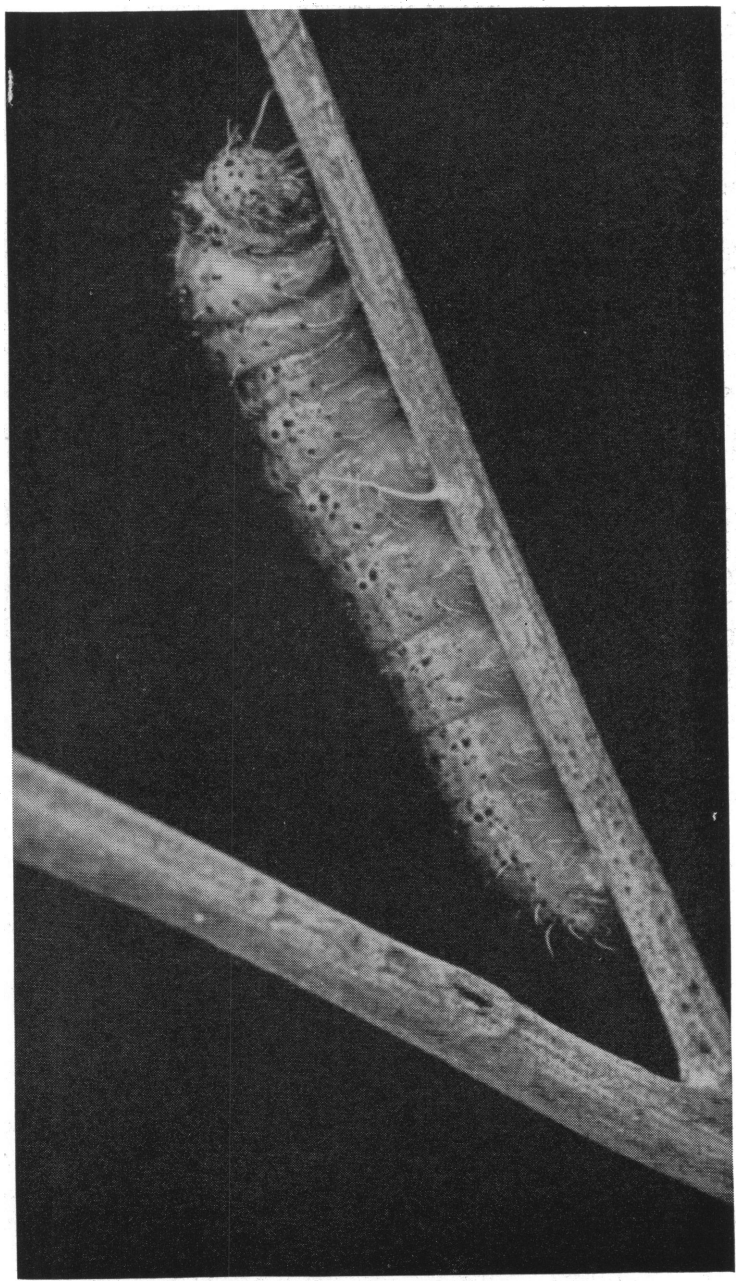

FIG. 7. Larva with silk thread.

body just below the thorax. In the following hours the animal will gradually become shorter and thicker, and the hump-like

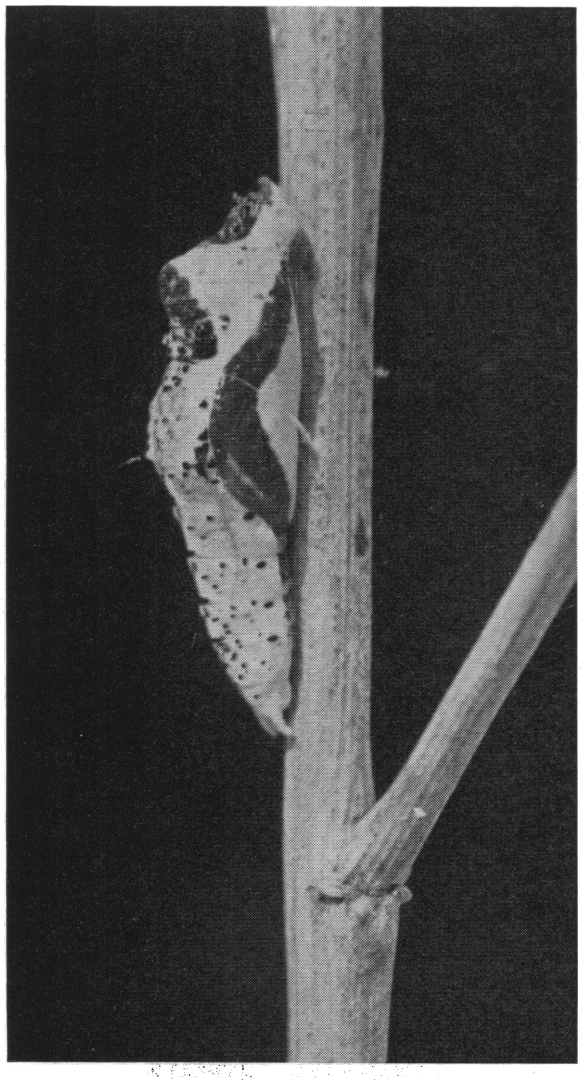

FIG. 8. Pupa on *Ambrosia* stem.

form of the thorax will be progressively more discernible. In nature the imago will normally appear within six to eight days after the larval skin has been shed.

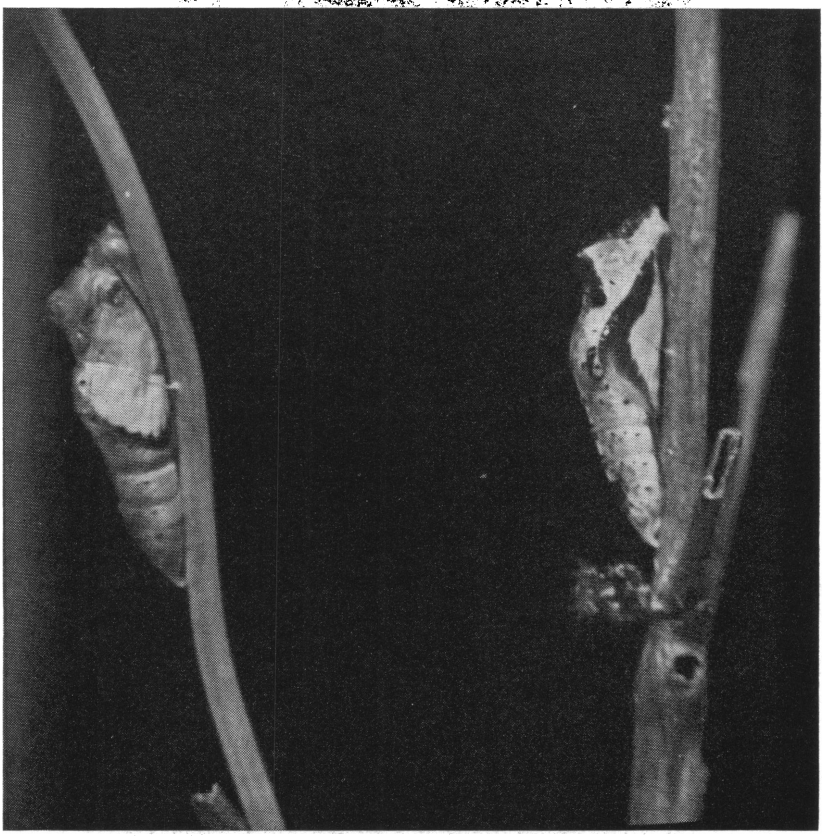

FIG. 9. Left: Totally green pupa on *Tropaeolum* stem. Right: Black and white pupa on *Ambrosia* stem.

The color of the pupa is very variable and seems to some degree to be dependent upon the color of its surroundings. The green pupae from *Tropaeolum* are markedly illustrative of this, especially as compared with the gray, white, and black pupae from the dry stems of *Eupatorium*.

IMAGINES

Observations during the mass outbreak at Fort Pierce Beach in May seemed to show that the females are hatched a little earlier than the males. Breeding experiments in the laboratory, however, have not given any confirmation of this.

The animals feed on all available flowering plants. We were not able to find a preference for any particular kind, with the exception perhaps of *Bidens*. But *Bidens* is, of course, one of the most abundant plants available all the year round in Florida, and it is moreover the favorite plant of butterflies and many other insects.

In the laboratory it is possible to keep the butterflies alive for some time by feeding them sugar water; the males live for four to eight days, the females twice as long. Observations in the field suggest a similar short life span; there is probably a preoviposition period.

Until about the middle of April all the individuals we found were white save for the typical black markings on the wings; after that date, all the females were more or less dark colored, indicating the variety *phileta*, though the coastal form seemed to have darker females than the ones from the inland population.

MIGRATIONS OF *ASCIA MONUSTE* IN THE SPRING OF 1949

Definition of Territory

We became especially aware of how limited the normal flying range of *Ascia monuste* is during our almost daily observations of the population on Hen Scratch Road, north of Lake Placid.

The actual breeding area was approximately 20 by 16 meters, situated between the road and the border of Lake Stearns, partly shadowed by eucalyptus and other large trees. Flying low over this area were usually about half a dozen butterflies, females with the short-turned, whirling flight so typical in egg laying, and males flying after them. Other individuals could be found in the vicinity seeking food on *Bidens* beside the road or on flowers in the scrub. Sometimes the circling around one another, which is an introduction to the mating, would carry a couple up to the tops of the trees.

A first glace of the colony may give the impression of a continuous going and coming of butterflies, but closer observation will prove this to be erroneous. The animals leave the breeding area for only short flights in the immediate neighborhood. As a matter of fact, we saw none more than 100 yards from the place where in all likelihood they had been raised.

This concept, that the butterflies are normally limited to a certain territory, was confirmed by observation at other breeding localities. Some of these localities were much larger and con-

tained many more individuals, and were therefore somewhat more complicated, but in each instance a close examination showed that the habitat consisted of a nucleus, with plants for breeding, surrounded by an area outside which the inhabitants did not go but inside which they flew around more or less casually.

First Records of Migration

On March 13, along the road at Craig on the Florida Keys, we noticed some whites flying, but only one or two at a time. Here, where the road is a sort of causeway, we observed several single individuals flying northward. They traveled so fast that we had difficulty in catching them. The flight was not only faster than normal but also more determined. There were but few flowers along the roadside, and it seemed remarkable that the butterflies seemed to ignore them.

One mile north of the Caloosahatchee River at Olga, where State Road 31 turns westward, a white butterfly was observed on March 20, crossing the road flying east-northeast. The vegetation here, as far as can be seen in all directions, is open flatwood pine forest without any flowering plants. In the ditches beside the road, however, *Bidens* and other flowers were present, but the butterfly crossed the road just over the flowers, ostensibly without paying attention to them, and continued its flight, which was in a remarkably straight line as far as it could be followed by the eye. We stayed at the place for more than half an hour but saw no more butterflies.

Just north of Okeechobee (1.5 miles north of the junction of State Roads 19 and 70) three or four white butterflies were seen on April 15 at 8:57 A.M. crossing the road at brief intervals, steadily flying towards 210° magnetic bearing.

The same day, between 9:25 and 9:55 A.M. (Eastern Standard Time), a stream of *Ascia monuste* was seen crossing State Road 68, 3.8 miles east of State Road 19, flying towards 210° magnetic bearing. The country is open here, and it is possible to watch the animals over a considerable distance. They appeared at the rate of one or two per minute, and the distance between them was so great that it is highly improbable they could see one another. Nevertheless they crossed the road within 100 yards or so of the same spot.

It seems justifiable to assume that the individuals seen north of Okeechobee were other individuals of the same stream, the tracks

coinciding perfectly. If the track had been extended southward over Lake Okeechobee it would have met the south coast in the neighborhood of Moore Haven. The populations at Moore Haven were first seen in the middle of February but disappeared during March. A week after the stream at Okeechobee was observed we passed through the Moore Haven area and again observed numerous whites, but we have, of course, no evidence of the origin of these animals.

If the track were retraced backward it would cross the east coast between Wabasso and Melbourne. Although in the afternoon we found numerous whites along United States Highway 1, especially between Sebastian and Roseland, no migratory movements were observed.

If it be assumed that the two streams observed April 15 north of Okeechobee are identical, these observations lead to an interesting conclusion: The two observation points are about 15 miles apart. We were not able to measure the ground speed of the animals, but we estimated it to be about 8 miles per hour. As the flight cannot have started before about 8:00 A.M. (Eastern Standard Time) on account of the temperature (see below) the individuals seen at Okeechobee before 9:00 A.M. must have started from a point between our observation points. This seems to indicate that this stream had started the preceding day, stopped during the night, and had resumed flight again in the morning.

Definition of Migration

The observations described above were of the behavior of butterflies outside their territory. We had no doubt that we were watching migrations, although on a very small scale. Later observations in the Fort Pierce area gave us a much clearer picture of migration, but before describing them it might be of value to define the term "migration" as used in this paper. A more thorough discussion of the phenomenon will be postponed to a later communication.

We use the term "migration" to describe a more or less unidirectional active movement of an insect outside its normal territory.

We are aware that in the field of vertebrate animals the term "migration" indicates a movement that includes a return of the animal to its original territory. We are furthermore aware that C. B. Williams, who has collected all available data indicating return flights in butterflies, is gradually becoming convinced that

return flights are characteristic not only of a few species but of a majority of the migrating species as well. This may be true, but we cannot consider it an established fact for any of the migratory species. It would therefore be more accurate to use such a term as "exodus" for the phenomenon in question, but the term "migration" is so commonly used that it seems inadvisable to change it. For insects the term should be used with the reservation that it does not include any indication of a return flight.

The whole problem of nomenclature for these movements seems to us of minor importance. When we acquire some insight into the physiological mechanisms of the movements a rational nomenclature must be established; on this point, however, we have as yet no knowledge for either vertebrates or insects.

Observations in the Fort Pierce Area

Mr. Brass first drew our attention to the Fort Pierce area. We visited the beach here for the first time April 2, and found a number of *monuste* flying around in spite of cool and windy weather. The same was true at Jensen Beach, especially on the west side of the island where there is mangrove.

On April 11, we found no butterflies here, but as we followed the road on the island south of the Fishing Lodge we found a number flying around just south of the old Coast Guard Station. It was here that, later in June, we found the butterflies breeding on *Cakile*. We also tried to follow the road north but that section had been destroyed by a hurricane some years ago, and the country was so difficult to travel, even in our "jeep," that we gave it up. We saw no butterflies there. On State Road 707 we observed three butterflies flying steadily south-southeast along the road, apparently migrating. At the south beach at Fort Pierce there were more butterflies, one or two traveling rapidly and unidirectionally south.

When we returned to Fort Pierce April 11, Mrs. Boone, proprietor of a gasoline station, suggested that we visit the north beach, because there at certain times of the year so many white butterflies appeared that "all the bushes looked like fruit trees in bloom."

As the following days were cool and windy, we did not return to Fort Pierce until April 15 (the morning of the same day we made the observation at Okeechobee referred to above). On the islands, especially on the north beach, on the bridges, and on the

mainland close to the bridges, enormous numbers of white butterflies were observed. They were not migrating but only flickering around and feeding on all sorts of flowering plants and bushes which they covered so thickly that they looked like cherry trees in blossom. Of 23 individuals caught, only three were females: one with small eggs, two with large eggs, in the ovary.

A female caught *in copula* had small eggs in the ovary. All the females were of a dark color (variety *phileta*). We observed no egg laying, nor did we find any eggs, larvae, or pupae. We followed the road north-northwest on the island and found that the number of butterflies did not diminish until about 5 miles farther north. Towards Vero Beach they were fewer in number, but at the same time we observed that the individuals were definitely migrating northward. North to Vero Beach, at least two streams were seen: one along the road and another just behind the dunes. On the road the butterflies passed at the rate of 22 individuals each minute. Streams were again found at Melbourne Beach, but the rapidly dropping temperature, which at 3:50 P.M. fell below 25° C., stopped the migration and the animals made interruptions to feed along the road.

The same day Mr. and Mrs. Lord, of the Fishing Lodge south of Jensen Beach, made the following observation: "About 7:30 A.M. unusually many individuals were seen, at 8:00 A.M. enormous numbers streamed in clouds towards the south. A colored man working in the garden had to brush them away to get working space. The stream covered the island six miles up to One Mile Bridge but were not found on the mainland. It lasted until 1:00 P.M. when it gradually stopped. The wind was weak from E or SE."

The next two days, April 16 and 17, were cool and, although a few directional flights were seen, they could hardly be described as migrations, as the animals continuously stopped for food or mating.

On April 18 we again observed migration on the beach north of Vero Beach. The same day Mr. and Mrs. Karl Hodges, of Indiatlantic at Melbourne Beach, reported as follows: "Today the southern whites have been flying along the Beach Highway, and seem to be in mass migration in reality to the north.

"About every minute, many in groups about seven feet from ground, 15 mph (about wind Southeast), warm, partly cloudy during day. Flying from about 11 A.M. to 4 P.M. and possibly longer.

"They are finding a place to settle for the night on the casuarina trees. Many on north side of some of trees as I write this."

On April 23 migrations were observed towards the south between Palm Beach and Stuart. North of Stuart they followed the beach but farther south they seemed mostly to follow United States Highway 1.

The intensity of the stream was rather low, about eight per minute. Fort Pierce Beach was inspected April 15, 16, 17, 18, 19, 23, 24, and 29. During these two weeks the number gradually diminished, so that on the last date the population was normal. There seemed to be nearly the same number of males and females.

From April 24 to 29 we inspected the area from Titusville to Stuart and found no real migrations in spite of favorable weather. Observers at Titusville Beach and at Cape Canaveral had not yet noticed any remarkable migrations.

In the first part of May only very few individuals were found at any place between New Smyrna and Miami. On May 10 a new outbreak started, and in the following week the number of individuals at Fort Pierce north beach rose enormously while it remained at the same low level at all other places between Vero Beach and Miami. The first day there were many more females than males; later, the reverse. On May 17 there were clouds of them at Fort Pierce, and the same day the migrations started in both directions along the shore. During the following days the streams increased in intensity until on May 20 streams up to 28 individuals per minute were observed. At the south beach the streams flew southward, and only 5 miles to the north they were headed in the opposite direction. On the neighboring part of the mainland were many butterflies, but we saw no definite migration.

General Conclusions of the Observations at Fort Pierce

It seems to us that the most striking feature of the habits of the butterflies at Fort Pierce Beach is that the hatchings of the imagines occur within a few days, over an area which is not so very large considering the enormous production of imagines but considerably larger than the inland colonies. In these we always found that the production of new individuals went on continuously; we always found eggs, larvae of all sizes, pupae, and imagines at the same time, and the number of adult butterflies remained about the same for long periods. At Fort Pierce we

had a very distinct maximum on April 15, and after the observation of the hatching time in the laboratory we could expect the next generation to come between 33 and 41 days later; the maximum of the next outbreak was May 20, 36 days after the first.

From these observations we conclude that the first requirement for a migration is a mass outbreak—a simultaneous hatching of a whole population within a few days. It may be asked if this is not a fiction. One might think that migrations also take place from smaller populations but escape notice because the individuals are few. This objection, however, does not fit in with our observations. From May 7, when we saw only three or four butterflies through the whole area at Fort Pierce, until the migrations started May 17, we made observations in the area every day except May 8, 14, and 15. Although we were looking especially for migrating butterflies we saw none. As soon as we had seen the migrations start, we traveled as far as Miami and returned slowly to meet the southgoing migration. This happened in the afternoon of the next day at Fort Lauderdale Beach where, in about half an hour, we saw six *monuste* flying south. The distance from Fort Pierce to Fort Lauderdale, following the coast, is about 100 miles, and as there can hardly be any migratory flights between 5:00 to 6:00 P.M. and 8:00 to 9:00 A.M. it may be assumed that these animals had left Fort Pierce early the preceding day when we saw the first migration heading north. The following day we found the southward migratory flights as soon as we reached Jupiter Beach and the northward flights at Vero Beach, both fully developed.

These observations have removed for us any doubt of the relationship between mass outbreak and migration. This relationship in itself of course provides no solution to the main problem: how and why the migratory reflex apparatus is activated. But it divides it in two: (1), how can the crowded conditions present at a mass outbreak activate migration, a problem that has a remarkable similarity to the problem of the effect of crowding on the development of the migratory phase in locusts; (2), why do certain populations develop mass outbreaks, or rather why do some populations have a continuous production of new individuals and why do other populations breed in waves.

Obviously, the first step in approaching this problem would be to examine the breeding areas of the population, but as already mentioned above we did not succeed in finding the breeding

grounds until May 17, the same day the second mass outbreak led to the first migration. We observed on that day, and repeatedly during the following couple of weeks, a great many acts of egg laying and found many eggs on *Batis* in the mangrove, but only once did we find two small larvae. Even when we carefully marked the egg-bearing plants and the position of the eggs, we were never able to find the larvae. The leaves showed no signs of having been bitten, nor were any droppings found. Generally we could not find even the eggshell. The newly hatched larva generally eats in captivity at least part of the eggshell, but in most cases some is left, especially of the base.

The number of adults diminished gradually and did not rise to a new outbreak in June, although single individuals were still seen during the last part of July. Nevertheless, upon removal to the laboratory the eggs from *Batis* developed normally and the larvae were easily reared on *Batis*, *Lepidium*, or *Tropaeolum*.

As we have as yet no evidence for what happened to the eggs in nature, we shall make no suggestions towards an explanation but will mention only that the phenomenon was not unexpected. From previous reports on migrations of *Ascia monuste* we knew that they are limited to the season between March and June.

REMARKS ON THE MIGRATORY FLIGHT

Of course it is not possible for us at the present stage of our investigation to approach the main problems of the migrations of insects generally, nor even of the species we are studying, but nevertheless we believe that some concluding remarks might be useful.

We have defined migration as a unidirectional active movement of an insect outside its territory. In addition to this theoretical definition, we wish to draw attention to some characteristic elements in the behavior and especially to those that enable the observer to decide whether or not a butterfly is migrating.

The Unidirectional Flight

The flight of a butterfly is always more or less flickering, but the observer will have no real difficulty in recognizing a flight as unidirectional. The migrations of *Ascia monuste* take place rather low, in heights of 3 to 10 feet above the ground, so that a person situated in the direction of flight can easily see that the flickerings are only oscillations along a certain direction. In a

flight of this kind, the best means of determining the direction is by the use of a field glass attached to a liquid-filled compass. With such a sight-vane placed at a point in the track it is possible to follow the animal and estimate the direction of flight within a few degrees.

Gunn and others in a recent publication (1948), in describing the flight direction of migratory insects, called attention to a very important point. They show the necessity of describing the direction and speed in relation not only to the ground but also to the surrounding air masses. They have proposed, therefore, the use of the same terms that are used in aircraft navigation:

TRACK: The direction in relation to the ground
GROUND SPEED: The corresponding speed
COURSE: The direction in which the animal is heading
AIR SPEED: The speed in relation to the air
DIRECTION: For the flight of the animal, the magnetic bearing (0°–360° mag.) towards which the animals are heading, or flying
WIND DIRECTION: The magnetic bearing from which the wind comes
WIND SPEED: Given, as with the other speeds, in miles per hour (mph)

It will be seen that the three velocities mentioned above can be considered as the three sides in a triangle, with the differences between the directions as angles. If we know two of the sides (e.g., ground speed and wind speed) and an angle (difference between track and wind direction) it is possible to construct the triangle and find the third side, i.e., the air speed and the course. (See fig. 10.)

The air speed, x, can also be calculated by means of the expression

$$x = \sqrt{(A \pm \sqrt{v^2 - d^2})^2 + d^2}$$

where A is the ground speed, v the wind speed, and d is equal to $v \sin c$, c being the difference in angle between track and wind direction. The plus sign must be used for $0° < c < 90°$ and $270° < c < 360°$, and the minus sign is valid when $90° < c < 270°$.

If b is the difference in angle between track and course, we have

$$\sin b = \frac{d}{x}$$

For values of c between 0° and 180° the course, s, is

$$s = t + b$$

and for $180° < c < 360°$, we have

$$s = t - b$$

Thanks to a suggestion in the paper by Gunn and others we have during our observations developed a method which allows

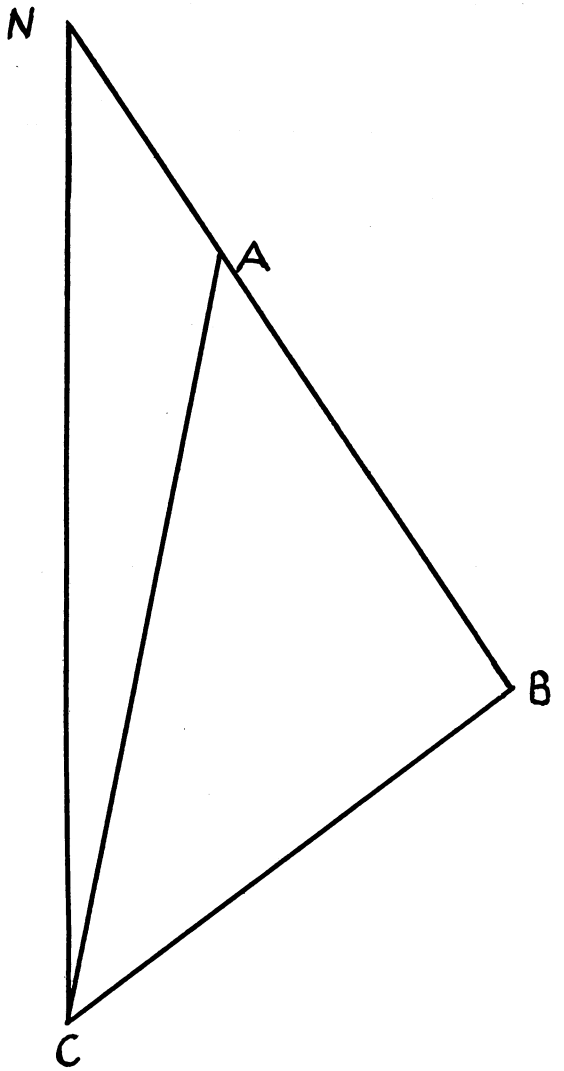

FIG. 10. Diagram to determine air speed and course. CN, degrees, magnetic bearing; angle NCA, track, degrees, magnetic bearing; angle NCB, wind direction, degrees, magnetic bearing plus 180°. If CA and CB are proportional to the speeds of the butterfly and the wind, respectively, then BA will indicate the air speed, and angle CNB plus 180° will be equal to the course.

us under certain conditions to measure the air speed directly and so check on the reliability of the measurement. So far we have made only three measurements of this kind. It is necessary to find a place where the track of the stream of butterflies passes over uniform and even ground (preferably along a road) for a distance of 1/2 to 1 mile. In the middle of the distance the windial anemometer is put up. In that end of the track from which the butterflies are coming, the car, with the cup anemometer attached to the windshield, starts at the same time as one of the migrating individuals and follows it over the distance. The distance is measured by means of the speedometer of the car, and the time is taken by a stop watch. Simultaneously the wind direction and wind speed are measured with suitable intervals on the windial. The magnetic bearings of the position of the windial and of the track are found by means of the sight-vane described above. The ground speed is the distance divided by the time in seconds multiplied by 3600. To reckon the air speed, the number of contacts of the cup anemometer is divided by the number of seconds and multiplied by 60. A direct observation of the course (the direction of the head of the butterfly) seems to be impossible to obtain.

By this method we made three determinations of the course and air speed, and later we checked the method by driving with constant speed, making the same observations as if the car were following a butterfly. This check was made on the road between Childs and Arcadia (State Road 70) where the country is open in all directions and the road runs on a straight 90° to 270° magnetic bearing for several miles. The results are given in table 1.

The expression "unidirectional flight" needs further explanation. As stated above, the flight is generally so straight, for as long as the eye can follow the animal, that a determination of the track can easily be made. On the other hand we have on several occasions seen the track change a little to conform to topography.

The numerous observations by Mr. and Mrs. Karl Hodges indicate that the direction of flights is always towards the south or north. In Florida most roads are orientated towards the four cardinal points except those along the coast which strike along or run at right angles to it. At Melbourne the coast and the roads vary about 20°, so that what are generally called north and south are really north-northwest and south-southeast. The essential point is, however, that all descriptions of previous authors—Ball

TABLE 1

Locality and Date	Track (degrees mag. b.)	Ground Speed			Wind		Air Speed				Course (degrees mag. b.)
		Distance (miles)	Time (seconds)	Speed (mph)	Average direction (degrees mag. b.)	Average speed (mph)	Contacts	Time (seconds)	Speed Observed (mph)	Speed Calculated (mph)	
State Road 70; 7/30/49	90	1.4	373	13.5	298	3.7	60	373	9.6	10.4	80
State Road 70; 7/30/49	270	1.0	257	14.0	318	3.0	76	257	17.7	16.2	278
State Road 70; 7/30/49	90	1.0	410	8.8	322	2.8	46	410	6.7	7.4	73
State Road 70; 7/30/49	270	1.0	432	8.3	328	4.4	93	432	13.0	11.3	289
Vero Beach; 4/18/49	0	.5	180	10.0	189	2.9	22	180	7.3	7.6	356
Jupiter; 4/23/49	180	.4	200	7.2	120	7.2	42	200	12.0	12.4	150
Jensen Beach; 5/19/49	160	.7	317	8.0	90	6.0	44	317	8.3	8.2	116

and Stone (1928), Fernald (1936, 1937a, 1937b), Stirling (1923), the Hodges as cited by Williams, *et al.* (1942), as well as ourselves (except for our observations at Okeechobee), and a few records of mass flights seen over the sea—have dealt with observations of migrations in Florida only along the coast. A closer examination shows that topographical features modify the direction. Individuals following the road on the island will follow it even if it changes direction slightly (5° to 10°). North of Palm Beach the coast line runs from north-northwest to south-southeast, and south of Palm Beach it runs north to south. Our observations indicate that the majority of the butterflies make this turn along the coast line, but there is a possibility that in some instances some continue the south-southeast track out over the sea.

We saw several individuals flying over Indian River (not migrating but flickering around), but we never saw a butterfly leave the coast and fly out over the ocean. Only in exceptional cases do they approach the ocean beyond the dunes.

Range of Migratory Flights

Our remarks on this are somewhat limited because we had no means of marking individuals, but assuming that all the migrations along the coast from April 15 to 20 and May 20 to 28 originated in the Fort Pierce area, which is probable, we are able to give some data.

During the migrations the northernmost point at which we found animals flying north was at Titusville Beach. The distance along the coast from Fort Pierce Beach to Titusville Beach is about 85 miles (135 kilometers); the southernmost point at which we found animals flying south was, as previously mentioned, at Fort Lauderdale which is a distance of about 100 miles (160 kilometers) from Fort Pierce.

At these end points the streams were very weak, with few individuals, and our observations showed that the streams gradually became weaker as they approached these points.

Although we must again stress the fact that we have no positive data concerning the range of migratory flights, we find it very probable that the range extends to approximately 100 miles in each direction, which represents about 12 hours of flight. This means that the migration lasts from one to two days of the five to six days (males) or 10 to 12 days (females) that constitute the normal life span of *monuste*.

The Migration as Mass Movement

It will be seen that the main characteristic of the migration is the unidirectional flight of the single individual. Generally, however, continued observations show that a number of individuals follow the same track. The migration therefore takes the form of streams varying in width from 10 to 100 yards. The intensity of a stream may be defined as the number of individuals per mile of the stream (S), and it can be estimated by counting the number of individuals (s) passing a cross section of the stream per minute and measuring the speed in relation to the ground (G). The intensity is then

$$S = 60 \frac{s}{G}$$

As we have found that G is rather constant in all our observations (in one case, 7.3; another, 10.0; five others, between 8.0 and 8.5 mph) no large error will be made in using s instead of S, as in many cases it will be difficult to determine the ground speed. We have found s to range from .2 individuals per minute to 30 individuals per minute.

Sometimes the animals appear singly, sometimes in small groups of two to five individuals separated by intervals. But in any case they behave quite independently of one another. It is especially instructive to observe a very weak stream, the individuals coming at such long intervals that it must be presumed they cannot see one another; nevertheless they behave very much in the same way.

As here described the migrations take place as narrow streams, but very often there is more than one stream going in the same direction, a few hundred yards apart. On the islands between Indian River and the ocean, where we made most of our observations, there were generally three streams, one along the dunes, one along the road, and one through the higher vegetation along the river. Generally the last one is not so sharply defined as the two others but is more diffuse.

Reflex Pattern of Migration

This is a part of the study of migratory habits which so far has been very much neglected, and we are not able to contribute to it beyond calling attention to certain facts that seem to have escaped the notice of previous authors.

For the butterflies living in a territory there seem to be four principal reflex patterns for the female and three for the males:

FOOD INTAKE: Common for both sexes
MATING REFLEXES: Different for males and females
EGG LAYING: Of course limited to the females
RESTING: During night and in cool weather, and basking in the sun, and cleaning, the same for both sexes

A further analysis of the behavior must await a later publication. For the present we wish only to point out that a butterfly in its territory always shows a behavior that can be referred to one of these four patterns. All flying around in the territory seems to be only "appetite behavior," in the sense of Lorenz, as introduction to one of the first three principal reflex patterns.

During the unidirectional flights outside the territory the butterflies seem not to have any of the normal principal reflexes. They do not stop to feed. Males and females travel side by side without taking apparent notice of each other. The flight is not an introduction to anything; it is a goal in itself. During migration the animals do not fly in search of a stimulus that may release a reflex; the flight is an independent reflex action. We still need to discover the physiological conditions for the corresponding "mood" (Stimmung) and the stimulus that releases it.

THE INFLUENCE OF PHYSICAL FACTORS ON MIGRATION

The following remarks are to be considered as only preliminary; our observations are too few and not detailed enough to permit elaborate conclusions.

Temperature is of major importance to migrations. We never saw fully developed migrations below 27° C. air temperature. In the morning the animals fly around and feed on flowers until the temperature of the air has risen to about 24° to 25° C. At that temperature some animals start to fly unidirectionally, but they may often stop to feed. As the temperature rises, the visits to the flowers become scarcer, and when the air is above 27° C. the migratory flight becomes typical in form. We also saw that dropping temperatures stop the migration at the same levels.

Our measurements have been too few to enable us to establish a relation between air temperature and the air speed of the flight. We have as yet made no measurements of the body temperature.

The migratory flight seems to be highly independent of the wind. We saw butterflies flying low and obviously taking advan-

tage of sheltering vegetation at wind speeds of 12 miles per hour across the flight, when this could be done without changing the general direction of flight. The direction of flight is determined more by topographical features than by the wind. As our few observations show more variation in the air speed than in the ground speed, it is probable that speed is regulated by visual stimuli as well.

Slight rainfall has no effect on the migration if the temperature does not go below 26° C. We made one observation during a heavy shower that stopped the migration (Jensen Beach, May 19) for a while. As soon as the sun reappeared the butterflies left the still dripping shrubbery where they had stayed and at once resumed the migration.

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