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Feeding behavior of Morpho butterflies (Lepidoptera: Nymphalidae: Morphinae) in a seasonal tropical environment*

by

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ABSTRACT: Observations in a semi-deciduous tropical wet forest in Guanacaste, Costa Rica, early in the dry season (December 1973) revealed that adults of the butterfly *Morpho peleides* (Lepidoptera: Nymphalidae: Morphinae) feed on tiny sap flows on exposed roots of the tree *Samanea saman* (Leguminoseae). These observations supplement earlier studies on the association of the butterflies with fallen, decaying fruits of the tree *Guazuma ulmifolia* (Sterculiaceae) in the same forest but during the previous dry season (January 1973). Morphoes collect in small groups of both sexes on the tree sap flows along with several species of ants. These feeding clubs, which are formed daily, usually in the afternoons, are tightly structured in that adults feed very closely together with no indications of agonistic behavior or courtship. When suddenly disturbed, the butterflies cease feeding and fly around the area before settling on nearby vegetation. The feeding behavior is different when morphoes feed on juices of *Guazuma* fruits: adults are widely dispersed and no feeding clubs are formed. *Guazuma* trees are more abundant in this forest and scattered over a larger area than the few *Samanea* trees. The association of *Pierella luna* with the tree sap flows and the conspicuous lack of *Caligo memmon,* both abundant butterflies, is discussed from the standpoint of phylogenetic relationship between the Satyrinae and Morphinae. The implications of the changeover in feeding behavior of *Morpho* are discussed in terms of seasonality and destruction of forests by agricultural practices. Experiments employing baits predict changes in the dispersion of the adult population at different times during the dry season.

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Behavioral responses of organisms can be very adaptive in that they provide the quickest means by which adjustments can be made to changes in environmental conditions affecting fitness, and if inadequate, they may eventually give way to more drastic response patterns such as physiological and genetic changes (SLOBODKIN, 8). Changes in behavior patterns in response to short-term changes in the environment provide collectively a unique mechanism of adaptive flexibility. This mechanism provides a different sort of adaptive response than that originating in genetic changes since, depending on the duration of an environmental change, individuals in a population may lag in a genetic adaptive response by one or more generations (LEWONTIN, 3). But behavioral responses can be extremely important forms of selection pressure during the early stages of an organism entering into a new adaptive zone or new ecological niche (MAYR, 4). It is precisely for these reasons that studies of behavior in the wild are important for understanding the mechanisms of adaptation in populations of selected animal species. Changes in the behavioral response of a given animal to, say, food can be brought about by changes in the availability of a preferred type of food. If local environmental conditions in the habitat result in a reduction in such a food source, the behavioral response may entail the switch to an alternative type of food which is more available at that time. If such a switch cannot be made, the animal is fated to either local extinction or forced emigration, which may be temporary or permanent. One might imagine that an animal living in a seasonal environment could be subject to the necessity of switching food if the food availability fluctuates in a seasonal fashion.

This study is concerned with the adult feeding behavior of the neotropical butterfly *Morpho peleides limpida* (Lepidoptera: Nymphalidae: Morphinae) in a seasonal lowland tropical forest in northwestern Costa Rica. An earlier report concerning this particular population of *Morpho* (YOUNG & THOMASON, 13) suggested that conditions of environmental stress, imposed by a severe dry season, have pronounced affects on demography of the species in this habitat. This present report discusses yet another aspect of this stress: seasonal changes in food sources exploited by adult *Morpho* result in a change in feeding behavior which very likely involves a switch from fruits to sap wounds on large forest trees.

As a group, the "morphoes" are among the most familiar and spectacular of the butterfly fauna in Central and South America. Although most species are generally associated with rather nonseasonal tropical wet forests (SEITZ, 7), *M. peleides* is known to inhabit very seasonal habitats in El Salvador and Costa Rica (YOUNG & MUYSHONDT, 12). Along with several other genera of forest-dwelling neotropical butterflies, mostly in the Nymphalidae, the morphoes feed primarily on a variety of rotting, sweet-odoriferous fruits and fleshy fungus growths on the damp floor of forests (7, 12), although the behavior patterns associated with feeding have not been explored. While this paper deals with observations of feeding behavior in adult *Morpho*, the implications of these studies may be of general interest with respect to how tropical seasonality affects the feeding habits of insects. There is evidence that the Costa Rican dry season alters the kinds of active insects in the community (JANZEN & SCHOENER, 2); small insects become inactive to avoid desiccation. But even large, robust insects like the morphoes can be expected to show changes in behavioral responses related to feeding, as food sources change with the advancing dry season.

There are several interesting applied implications of this study for tropical entomology in general. First, there is the question of how seasonal climatic changes affect the feeding behavior of insects, and more importantly, how such changes affect insects that feed on plants or plant products. It is known that trees in the tropics are affected in various ways by seasonality (2), and seasonality may induce insects to changeover in foods as seasons change, and this may involve changes in nutritional intake in different seasons. This particular study has even other implications for applied studies since the insects in question were confined to a forest habitat isolated from other similar habitats as a result of agricultural practices: it is a confined population of an insect that is dependent upon food items produced by tree species and not only have many of these trees been removed when the land was cleared, but even today there is continued selective removal of trees from the remnant forest itself. The *Morpho* butterflies present a very different problem of adaptation to man-made tropical habitats in that they depend upon food items other than flowers, which contrasts with *Precis* butterflies in Africa, where they feed on various flowers in gardens (OWEN, 6).

MATERIAL AND METHODS

The site for these studies, the "Barranca forest", in the tropical dry lowlands of northwestern Costa Rica is unique in that it is a small area of semi-deciduous tropical forest (about 900 × 500 m) surrounded by open pasture (Fig. 1). A rather pronounced dry season usually begins in early November and lasts through May, during which time many large trees lose their leaves and cease vegetative growth (5). A good description of this small forest is given by ORIANS (5). The forest supports a rich fauna of insectivorous reptiles and birds, and many of the nymphalid butterflies that are active near the forest floor are usually wary when approached with a net, probably attributable to severe predation pressure by these small vertebrates (YOUNG, 11). The butterfly fauna associated with rotting fruit and tree sap flows includes *Prepona, Hamadryas, Anaea, Historis, Victorina, Caligo, Opsiphanes,* and *Satyrinae* in addition to *Morpho.* The forest floor is covered by a dense layer of leaf litter (Fig. 2) that renders most of these butterflies very cryptic while feeding on or near the floor.

During a short period of eleven days in January of 1973, casual observations were made on the feeding behavior of *Morpho* on experimentally-placed banana baits (see YOUNG & THOMASON, 13 for the details of this experiment) as part of a demographic study of this insect and a search was made for their natural food sources. At this time many trees forming the forest canopy had already lost their leaves, the ground was hard and the leaf litter very dry. Observations on adult behavior at food sources included evidence, or lack thereof, for (a) agonistic interactions among adults of the same and opposite sex, (b) agonistic interactions of *Morpho* with other butterflies on the food, (c) courtship in *Morpho,* and (d) communal feeding.

The Barranca forest was revisited during the following December (1973) for the purpose of exploring the feeding behavior of *Morpho* during the initial stages of the dry season; these observations could then be contrasted with those from the previous January. From December 12 through December 25, 1973, feeding behavior was observed for a total of seven days. At this time the canopy was still full and the forest floor was just beginning to become hard. The last rains had ceased about five weeks prior to these observations, a date which corresponds very nicely to the cessation of rainfall the previous year. The same type of field observations were made during this second period of study. At this time these butterflies fed exclusively on tree sap associated with tiny wounds on exposed roots of a large canopy tree (Fig. 2), *Samanea saman* Merrill (Leguminosae). Despite extensive observation in the forest during the previous January, there were no instances of *Morpho* or other fruit-eating butterflies feeding on tree sap wounds at that time. Large areas of the forest had been canvassed for this purpose and only one natural food of the butterflies was found (the decayed fruit of the tree *Guazuma ulmifolia* Lam. - Sterculiaceae). With the discovery of *Morpho* on tree sap wounds of *S. saman,* observations were limited to this "feeding site" in the forest; the observations on each of seven days were usually at 8:00 AM, 10:00 AM, and again between 1:00 and 3:00 PM. At each time, the sap wounds were approached very quietly to study diurnal patterns of feeding and a count of the morphoes of each sex was made; it is easy to distinguish sexes as the female possesses a series of white dots on the ventral sides of the forewings. During two of the days of study (December 24-25, 1973) the feeding behavior of *Morpho* was photographed with minimal disturbance. On one day when observations were not made, the tree sap wounds themselves were examined for exudate and for the presence of other insects. At other times searches were made for other food sources being used by *Morpho.*

Previous experience with *Morpho* allows one to determine the approximate age of adults according to the amount of wing damage. As the butterfly ages, the wings become brittle and they begin to tatter and lose scales. When observing adults feeding during the December study period, it was noted whether they were "fresh", "middle", or "old". The tatters in the wings are easy to see at a distance, and with care and practice, one can approach the feeding butterflies to within a meter for closer scrutiny of sex and age. This method of aging adults is by no means accurate, but it does allow one to distinguish in a reliable manner very young ("fresh") individuals from other age groups. It is thus possible to determine if the population is producing new adults during the period of study.

RESULTS

During the dry season (January) *Morpho* feeds on the decaying fruits of *Guazuma ulmifolia* (Fig. 3A). Many of the blackened fruits can be found in the seed shadow of the parent tree and upon close inspection, each fruit is covered with a thin film of sticky, sweet-smelling substance. But the odor is noticeable to the observer only when the fruit is held to the nose. The decaying fruit is present throughout most of the dry season after December and it is likely the only food source of *Morpho* during this period, but butterflies readily come to experimental baits of rotting, crushed banana.

Early in the dry season (December) adult *Morpho* feeds at tiny sap wounds on exposed roots of *Samanea saman,* either singly, in twos, or in larger groups (Fig. 3-5) The sweet odor of the wounds is only detectable when the nose is placed against it. If banana baits are placed out in the forest near this feeding site (about 15 m away), *Morpho,* along with *Caligo,* comes to these within a few minutes. But if such a bait is placed next to the tree wounds (about 1-3 m away), *Morpho* invariably goes to the latter and ignores the banana; *Caligo* is never found on the tree sap wounds. The satyrid butterfly *Pierella luna luna* is often found on the tree sap wounds but seldom on the banana (Fig. 4A). Other members of the fruit-feeding ensemble of nymphalid butterflies present in this forest are not found on tree sap wounds but all of them readily come to banana baits. *Pierella luna* is also found on the fruits of *Guazuma* but not the others. At least one species of *Trigona* bee is found daily in large numbers at the sap flows. During December when *Morpho* feeds on the tree sap wounds of *S. saman,* the developing fruits of *Guazuma* are still green and there are few or no fallen fruits on the forest floor.

That *Morpho* is actually feeding on *Guazuma* fruits, and liquids associated with wounds on the big roots of *Samanea* is indicated by the observation of the proboscis contacting the substrate (Fig. 5). Furthermore, as feeding continues, there is an accompanying movement of the proboscis in a probing manner for fresh places on the substrate. When the butterflies feed on rotting bananas, there is a noticeable expansion of the abdominal body wall resulting from the prolonged intake of large volumes of liquid. In the two natural foods in question, the liquid component consists of a thin sticky film that does not have the watery consistency of juices from the banana bait, and therefore the abdomen does not become distended.

Although the tree sap wounds are very small (about 8-10 mm across), several adults of *Morpho* can feed simultaneously at each one (Fig. 4). The actual wound is a small cleared area where the bark has been scraped away (Fig. 5) and the exposed tissue is sticky to the touch. There are no large accumulations of fungus growth on the wound, although it has been observed elsewhere in wetter Costa Rican sites that *Morpho* feeds on juices associated with growth of slimy fungi on trunks of fallen *Cordia* trees (12). The actual feeding mechanism for taking up nutrients from sticky substances associated with tree wounds or fruits is not known for *Morpho,* although owing to the highly viscous condition of the substances, a liberation of digestive juices from the proboscis may be involved. Without such an adaptation it apparently would be very difficult for these butterflies to exploit such viscous food sources. In this context, it is again interesting to note that I have seen only *Morpho* and *Pierella* feeding at these sap flows, perhaps to the exclusion of many other butterflies that may be able to exploit only more watery substances.

Feeding behavior in *Morpho* involves a lack of aggressive interactions among adults when several are present at the same time. The butterflies are spaced out individually on different *Guazuma* fruits with little or no close interactions. Although conditions are often crowded on tree sap wounds (Fig. 4), there is a noticeable lack of aggression during feeding. In fact, two adults of the same age and sex can be so close to one another that their probosci actually come into contact while both are feeding (Fig. 4B). When another butterfly arrives at a "feeding club", there may be some wingflapping of settled individuals, but seldom do they cease feeding.

Thus "feeding clubs" are created by the simultaneous feeding of two or more butterflies at a single sap flow or among two or more sap flows very close to one another (i.e., within 2-3 cm) on the same root (Fig. 4). Both sexes participate and there are no overt gestures of courtship within the club. I have noticed that occasionally a male will attempt to mount a second male by sliding between the closed wings from behind. This behavior usually results in both males settling down again for feeding. It only occurs when there are several adults feeding on one sap flow, and therefore the behavior may be induced by crowding. Feeding clubs are very temporary associations, in terms of membership and size. They very likely are the result of two factors: the necessity for several butterflies to feed together on a type of food supply that is very limited in the forest, and the reinforcement of landing at the same food patch through visual stimulations of a cruising butterfly by the wing movements of one or more butterflies already on or near that food. The conspicuous blue iridescence of the upper surfaces of the wings function to attract conspecifics in *Morpho.* (YOUNG, in preparation), and it may be a powerful means of recruiting individuals to a resource in forests. If the feeding club is suddenly disturbed, all of the butterflies take to the wing and flutter in circles over the feeding site; within a few minutes, all of them settle on nearby understory vegetation and forest floor. The initial intermingling of several morphoes in flight just above the feeding site is an explosive event: several shimmering and dazzling-blue, large butterflies "spring up" from the forest floor. This behavior is reminiscent of a "predator-confusion" syndrome.

Another factor that may be involved in the formation of feeding clubs is the tendency for many butterflies in the population to feed at the same time of day in this habitat. There is greater feeding activity during the early afternoon (13) on *Guazuma* fruits and crushed banana during January, and on *Samanea* sap flows in December (Table 1). Thus the adults do not feed throughout the day, but rather concentrate their activity into rather discrete periods. The feeding clubs are largest between 1:00 and 3:00 PM (Table 1) and they contain both males and females. Males are usually more abundant than females at feeding sites, despite a sex ratio of unity witnessed in large groups of eggs (12). The difference is clearly behavioral, with females being more secretive in their habits than males. Oviposition tests with captured females taken from feeding clubs (a total of 5 were tested for fertile eggs—see YOUNG, 11 for the technique) indicate that both mated and unmated females are found in these aggregations.

TABLE 1

Feeding ensembles of adult Morpho peleides *on a sap wound of an exposed root of the tree* Semanea saman *(Leguminosae) in the "Barranca site" forest, Guanacaste, Costa Rica**

Date	Time	"Fresh"		"Middle"		"Old"		Total	
		♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Dec. 12, 1973	8:00 AM	0	1	0	1	0	0	0	2
	10:00 AM	1	0	2	0	0	0	3	0
	1:00 PM	2	0	3	2	0	0	5	2
Dec. 13, 1973	8:00 AM	0	2	0	0	0	0	0	2
	10:00 AM	0	4	1	3	0	1	1	8
Dec. 16, 1973	1:30 PM	1	0	0	4	0	1	1	5
Dec. 17, 1973	8:00 AM	0	2	0	1	0	0	0	3
Dec. 22, 1973	1:00 PM	1	1	0	0	0	0	1	1
	2:00 PM	1	4	1	1	0	1	2	6
Dec. 23, 1973	1:00 PM	1	5	1	0	0	1	2	6
	2:30 PM	0	3	1	1	0	0	1	4
Dec. 24, 1973	1:00 PM	1	2	1	2	0	1	2	6
	2:00 PM	0	7	1	6	0	1	1	14
	3:00 PM	1	9	1	7	0	3	2	19
Dec. 25, 1973	1:00 PM	0	3	1	1	0	0	1	4

(*) Fig. 5.

In fact, one female was so fresh in appearance that she must have been only an hour or so old. It is unlikely that the feeding club represents a social unit that enhances the likelihood of successful mating within the immediate vicinity of the food. Feeding females are very unreceptive and remain very still, with their wings kept tightly shut. Wing flapping in the sexually-dimorphic *M. peleides* is an important signal given by females during the initial stage of courtship behavior in cages (Malcolm Barcant, pers. comm.).

Feeding clubs are composed of adults of different ages and during December there is a predominance of fresh adults (Table 1); the numbers of old adults are low. This trend in age-structure, also seen later in the dry season, has been ascribed to increased vulnerability of these weakened butterflies due to predation by small vertebrates and to increased mechanical difficulties in flight (13).

The frequency of formation of feeding clubs during December may be related to the number of feeding sites available. One aspect of this question is the attractiveness of sap flows on different tree species to the butterflies. Very few data are available on this, but from preliminary examination, it is unlikely that many species are preferred. In fact, feeding may be limited to a few leguminous genera in addition to *Samanea.* Another consideration is that the sap flows may originate from the biological activities of other animals on the forest floor. Small sap wounds on forest trees can be the result of a variety of environmental agents, including abrasion, scraping activities of birds and mammals, and biting activities of insects. Several different ants visit the sap wounds along with *Morpho;* there are three abundant small species: *Paratrechina* (*Nylanderia*) sp., *Cyphomyrmes* sp., (*rimosus* group), and *Pheidole* sp. In addition, the larger ant *Dolichoderus* (*Monacis*) *bispinosus* (Olivier) is also present in small numbers. The intriguing possibility exists that the sap wounds visited by *Morpho* are actually "ant tracings", produced by some or all of these species by the scraping away of thin layers of bark in search of carbohydrates. If this is true, then the feeding clubs of *Morpho* are created by the foraging activities of the ants. If the sap flows are ant tracings, then this food type may only be available at certain times of the year and entirely absent at others, depending upon seasonal changes in foraging activities of the ants. The same is true if the sap flows are produced by some other animals (birds), and only secondarily visited by ants. Small creepers peck at the large exposed roots of forest trees for a variety of reasons and may create the wounds. Owing to their size and appearance, however, it is very likely that the sap flows are produced by ants (or birds) and not from mechanical abrasion of branches, litter, etc.

The sap flows provide a food source for many *Morpho* butterflies over a two-week period (Table 1) and probably for a considerably longer time. Undoubtedly the butterflies receive carbohydrates from the sap. It is interesting that during the previous January we did not see any instances of *Morpho* feeding on sap flows, despite intensive field work in that part of the forest where this behavior was to become so evident the following December.

DISCUSSION

In seasonal tropical environments, food sources may change for animals over relatively short periods of time and necessitate changes in feeding behavior. Natural selection would favor such "adaptive shifts" of behavior since animals that fail to change could suffer a reduction in fitness from several sources including (a) outright mortality and massive loss of genotypes, (b) reduction in mating success due to weakness from reduction in food, and (c) reduction in egg production by the average female in the population. Life span may also decline for the average adult, perhaps reducing the amount of time available for courtship and egg-laying. All of these factors are important for many organisms. In relatively non-seasonal, wet-tropical environments, less food stress among adults occurs since moist, readily accessible nutrients are present throughout the year (i.e., slimy fungal growths, decaying fleshy fruits, carrion, etc). The nutrients in such foods are probably easier to imbibe than those in the viscous foods of *Morpho* in the Barranca forest. Under less stressful conditions, which for *Morpho* have been shown to affect population size (10, 13), larger populations are expected. In a very seasonal environment, larger adult populations are predicated for the wetter months if more accessible foods are available, and if the butterflies make a shift in feeding behavior.

The present findings suggest that even within a period of stress (dry season), there occur shifts in feeding behavior in response to temporal changes in potential food. The butterflies do respond to changes in food-types, revealed by the very fast appearance of the insects on the fleshy, rotting bananas placed in the forest, and also by the transition from *Samanea* sap flows to fallen *Guazuma* fruits as the dry season advances. In fact, the very fast discovery of experimentally-placed baits by *Morpho* and other butterflies is indicative of a stressful environment. Assuming that the banana odor does not block the sensory perception of other foods, the quick appearance of these butterflies on the bait and the fact that the same individuals often return to a particular bait day after day (13) indicate that other (natural) foods are in limited supply. The observations of *Morpho* and *Pierella* feeding on the *Samanea* sap flows, even when banana baits are placed nearby, indicate that the highly odoriferous properties of the banana do not necessarily block sensory perception of other foods. Even when the butterflies are baited near fallen *Guazuma* fruits, many individuals feed on the natural food (13). An intriguing extension of these observations is the possibility that *Morpho* and others can eventually shift from a viscous natural food to a more watery experimentally-placed food such as bananas. If bananas are easier to imbibe and if they contain the same or similar nutrients needed by *Morpho* as found in natural foods, such ability could be adaptive. In fact, such a shift might occur with natural foods if watery foods become abundant during wetter months in the Barranca forest: there may not be a complete changeover of available foods (i.e., sap flows may occur during the wet season as well) but rather the insects switch over in feeding behavior. Adults of *Morpho* become very abundant during July and August in the Barranca forest and they do not feed on *Samanea* sap flows or *Guazuma* fruits during these wet months.

As food becomes more limited in the habitat, both in patch size and distribution of the patches, selection should favor the expression of cooperative or communal feeding behavior so that several individuals can feed successfully at a given patch. This should be the case since the likelihood and amount of energy involved in locating a different food patch by a foraging individual become very critical factors in the feeding behavior: the likelihood declines and the amount of energy increases. Both conditions favor communal feeding if individuals are to avoid mortality due to starvation during a stressful period. A bonus of communal feeding behavior is that conditions are established for "predator confusion" syndromes associated with the disbanding of a feeding club by a sudden disturbance. Such behavior is only adaptive if *Morpho* is palatable to vertebrate predators. If other factors favor the temporary banding together of these butterflies for feeding on a patchy resource, confusion flight behavior increases the chance for escape of individuals when a feeding club is found by a predator. If alternative food patches are very easy to find with minimal expenditure of energy, selection might favor the expression of agonistic behavior in the adults at any one food patch. This would be a means of reducing intraspecific competition for food when in fact food is abundant as a patchy but accessible resource. But when food patches are few and widely scattered, as presumably the case for *Samanea* sap wounds, many individuals in the population will feed in a single or few patches and communal feeding will be expressed. Agonistic behavior was not observed at these food sources.

The formation of the *Samanea* sap wounds used as feeding sites by *Morpho* and the relationship of the numerous ant species to them remains unresolved. On New Guinea, several species of *Paratrechina* nest on the floor of the tropical rain forest and workers of at least one species, *P. longicornis*, abundant in many tropical regions, feed at sugar baits (WILSON, 14). Very little is known about the biology of *Cyphomyrmex* although the primitive position of this genus within the Attini is of considerable interest owing to the fungus-culturing habits of a more advanced genus, *Atta* (14). One wonders if minute fungal growths associated with the the sap flows are the food source of these ants. At least one species of *Monacis* (*M. debilis*) collects honeydew from membracids and the presence of *M. bispinosus* at sap flows may indicate foraging for sugars. The feeding habits of *Pheidole* are diverse (17). All of these observations suggest that the ants present at *Samanea* sap flows are feeding, but the question of whether or not some or all of these ants actually create the feeding sites ("ant tracings") is unresolved.

Feeding occurs at various hours of the day, but the largest feeding clubs at *Samanea* trees are during the mid-afternoon. Especially during the dry months, the hottest hours of the day are in the early and middle afternoon, and feeding can result from several selection pressures including feeding at hottest times to avoid desiccation associated with flying, postponement of feeding until after other activities (courtship, oviposition) have taken place, and feeding during hours when forest floor predators are least active. No data are available to support any of these hypotheses, which are not mutually exclusive. The most attractive explanation is probably a combination of the first two. Both *Morpho* and *Caligo* are large, dark-colored insects and perhaps heat up very quickly in sunshine. For *Caligo* the problem may be more acute since both sides of the wings are very dark and generally non-reflective, thus facilitating the uptake of heat. In *Morpho* the ventral sides of the wings are non-reflective and dark while the upper sides are dark but reflective for the most part. *Caligo* shows a very pronounced bimodal feeding pattern in the Barranca forest, with peaks occurring before 8:00 AM, and after 4:30 PM during the dry season. This diurnal pattern of adult feeding behavior in *Caligo* may therefore be a more extreme adaptation for avoiding desiccation and over-heating from large heat uptake due to the large surface area of the wings. For *Morpho,* with a presumably less thermoregulatory problem, there is but one major peak period of diurnal feding in which the insects become less active during the hottest part of the day. Feeding with the wings closed in the shaded understory of the forest allows them to escape high temperatures.

The apparent lack of *Morpho* feeding on sap flows later in the dry season could either be due to an outright decline in the number of these food patches or increased desiccation rates of these patches, making them very temporary resources for insects. As the dry season advances, wind penetrates deeper into the forest and desiccation rates on a variety of substrates are expected to increase. Nutrient solutions associated with crevices of more textured substrates such as fallen *Guazuma* fruits retain this moisture longer than smooth surfaces, thus providing a more permanent food source for insects at the height of the dry season.

Clearly the feeding niche of *Morpho* in the confined Barranca forest includes the exploitation of viscous films of nutrients on at least one fruit and one type of tree sap, and there is a succession within weeks from one resource to the other. There is a shift in food that involves a change in feeding behavior from solitary to communal associations at food patches. It is likely that both foods are not the most efficient (in terms of the ability of butterflies to eat them) for butterflies such as *Morpho*: adults will feed on crushed bananas when brought into the laboratory and offered this food immediately after a feeding spell on *Guazuma* fruits or *Samanea* sap flows. But individuals that have fed on banana in the wild will not feed immediately on this same food in the laboratory, suggesting that less nutrients are ingested per unit time (along with water) from viscous foods than from bananas, so that in fact the dry season foods of *Morpho* are "stress" foods; during the rainy season there are more watery resources for these and other insects. However, there are two additional interpretations of these observations that must be examined before confirming this conclusion: the butterflies may habituate to a particular food item and will resume feeding only if a different food item is offered; and they may cease feeding when their abdomens become sufficiently distended. It is also possible, that despite the fact that banana juice causes rapid abdominal distension and subsequent cessation of feeding, this food item may, in fact, contain less nutrients than natural food items. Banana juice may be mostly water, and analyses are needed on its nutritional contents compared to that of *Guazuma* fruits.

I believe these findings on the feeding behavior of *Morpho* during the tropical dry season have further implications for yet another aspect of the behavioral biology of neotropical nymphalid butterflies: the behavioral patterns for feeding described bear on the question of phylogenetic relationships within the Morphinae and between this subfamily and the Satyrinae. This problem has been discussed for the relation of *Morpho* with the satyrids *Caerois* and *Antirrhea* (VANE-WRIGHT, 9). It is argued that *Morpho* and *Antirrhea* may be very closely related owing to similarities in adult scent organs, and in the shape of the egg. Vane-Wright (pers. comm.) has also argued that *Caligo* (in the Morphinae) is not closely related to *Morpho* owing to departures in egg shape and adult scent organs associated with courtship behavior. It is therefore very interesting to note the apparent similarity in food preferences between *Morpho* and *Pierella* in this study, and the absence of *Caligo* on both of the viscous foods under observation. The similarity of adult feeding behavior between *Morpho* and *Pierella* (along with other characters) presumes a close phylogenetic relationship of Morphinae to Satyrinae. The ability of *Morpho* and *Pierella* to feed on these foods to the apparent exclusion of *Caligo* and perhaps others provides further support of Vane-Wright's view with different data from another satyrid genus. This behavioral divergence involves morphological and physiological adaptations for exploiting a highly viscous food; all of the butterflies can feed on watery foods such as bananas, but apparently only some (*Morpho* and *Pierella*) have exploited a different type of food. The ecological implications here are clear: assuming that food is limited, interspecific competition among members of the butterfly ensemble exploiting rotting fruits provides selection pressure for some members to enter into a new adaptive zone for feeding.

Finally, the observations permit a speculative glimpse at the "feeding strategy" of *Morpho* that is useful as a starting point for further behavioral studies of considerable general interest. For example, clearly one of the major forces of natural selection operating on any animal population of a mobile species is how individuals obtain sufficient food for survival and reproduction when this resource is distributed patchily in space and/or time in the habitat. Individuals must locate food patches and retrieve nutrients from them, and the type of feeding behavior expressed will be determined by how this problem is presented to the species. For *Morpho* in the Barranca forest, at least two cases of this problem are apparent: Case I - a food resource is distributed spatially as numerous large patches and this resource is only seasonally available. This case is exemplified by fallen *Guazuma* fruits: *Guazuma* trees are numerous over a large portion of the Barranca forest and the crown of each tree is large; many of the fallen fruits stay beneath the parent tree. Such a resource distribution in space favors a highly dispersed butterfly population with minimal or no communal feeding behavior. Case II - a food resource is distributed spatially as a few small patches; it is rare and hyperdispersed. An illustration of this case is *Samanea*: this tree is rare, not all individuals will have sap flows, and sap flows may or may not be seasonally available as feeding sites for insects. Such a very spatially patchy resource with small patch size favors the expression of communal feeding in adult *Morpho* with an increased likelihood for considerable interaction among butterflies in feeding clubs. But increased interactions among butterflies, be they related to courtship, predator-defense, or play, do not include aggressive encounters since selection would disfavor such behavior up to a certain local population density. If local population density becomes very high, then selection would favor increased dispersal and behavioral patterns promoting aggregation would dissolve. Clearly the point at which this would happen is determined by the life history pattern of the butterfly.

As trees are continually removed from the Barranca forest as a result of increased activity by local farmers, there may approach a time when such activity will alter the feeding behavior of *Morpho*. As *Guazuma* trees, for example, become scarce, Case I above becomes an unlikely food-exploitation pattern, and it may force the *Morpho* population to adopt the Case II strategy with this food item. If the few *Samanea* trees are removed, this would exclude the Case II strategy on that food item for the *Morpho* population. Clearly, these predictions are examples of how destruction of a tropical forest could alter the feeding strategy of a butterfly population that does not exploit flowers. Unless the butterflies can changeover to other food items not being reduced in number by agricultural practices such as lumbering, the eventual result would be local extinction of the species if emigration was not possible. Thus not only is the destruction of larval host plants an important factor in the survival of butterflies in disturbed tropical forests, but clearly the adult food sources are also determining factors. In fact, for *Morpho peleides,* whose larvae feed on several legumes in forest habitants (12), the greatest stress for survival is likely to be placed on the adults owing to their dependence on fruits, sap flows, and fungi as major food items.

These predictions have implications for establishing a system of experimental baits in a confined forest habitat. If piles of bananas are distributed evenly over the forest during December (when feeding is primarily on *Samanea* sap flows) active adults of *Morpho* will chance upon patches of this new food source and the pattern of dispersion would change from Case II to Case I. If the same experiment is done during January (when feeding is on *Guazuma* fruits), there will be little or no change from the Case I pattern. At this time, however, the butterflies would probably shift from *Guazuma* fruits to bananas. If it is assumed (as argued in this paper) that morphoes prefer bananas to *Guazuma* fruits, an experimental study of placing small, dispersed patches of bananas in the Barranca forest during January might induce communal feeding by individuals feeding separately on natural fruits. Such shifts in feeding behavior will alter the pattern of gene flow since breeding takes place during the dry season (13).

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Fig. 1. General view of the forest habitat where the feeding behavior of adult *Morpho peleides* was studied during the dry season. (Barranca forest, Guanacaste Province, Costa Rica).

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Fig. 2. The forest tree, *Samanea saman* (Leguminosae), whose large exposed roots have small sap flows used as feeding sites by *Morpho* and other insects (December 23, 1973). Feeding adults of *Morpho* lie still against the leaf litter.

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Fig. 3. A. Decaying fruits of the tree *Guazuma ulmifolia* (Sterculiacae) that are used as a food source by adult *Morpho* in the Barranca forest during the late dry season. B. fresh male feeding at a sap flow on a root *of samanea saman* (December 24, 1973). C. two fresch males feeding together at a *Samanea* sap flow (December 24, 1973).

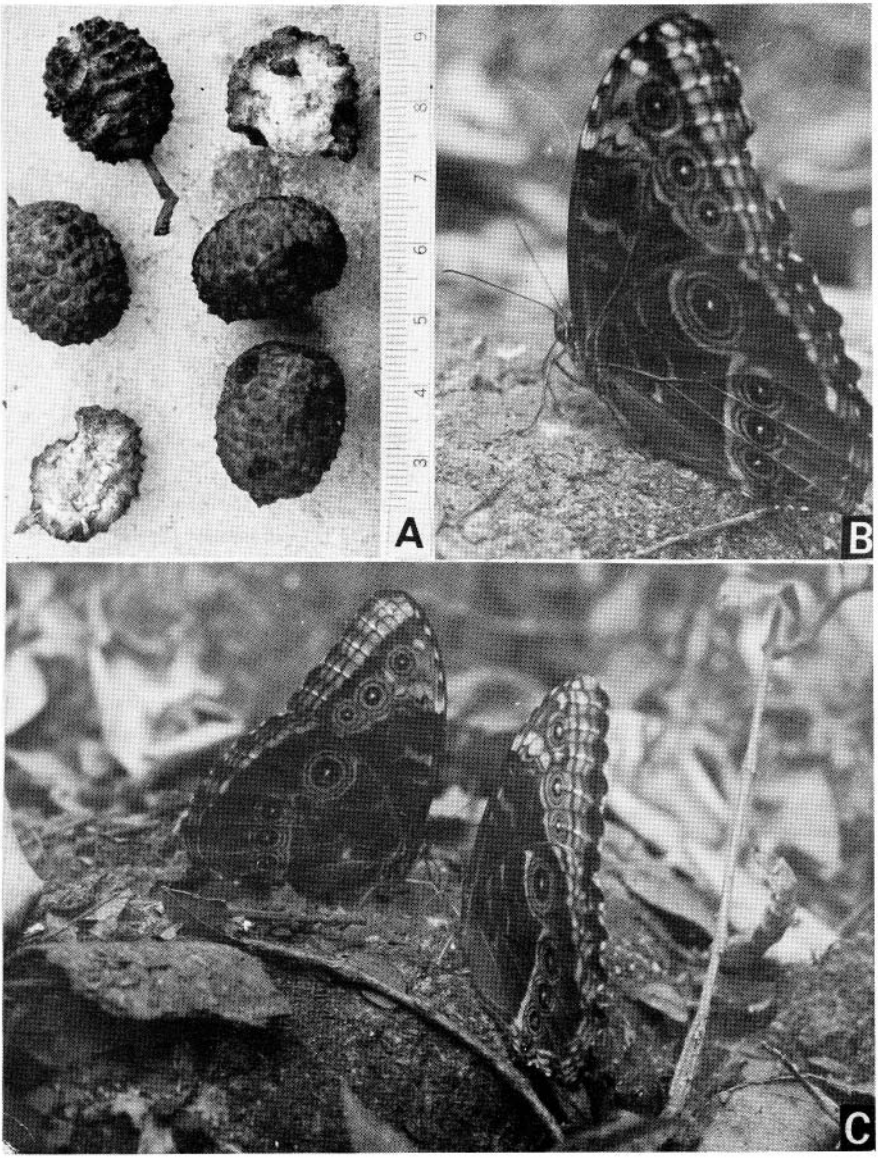

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Fig. 4. A. A feeding club of five morphoes in addition to a single individual of the satyrid *Pierella luna* (upper right) on two sap flows on a root of *Samanea* (December 25, 1973). B. A close-up view of two adults of *Morpho* feeding at a single sap flow (same date). The white area beneath the legs of the individual on the right is the food. Note the very close proximity of these individuals and the positions or their antennules.

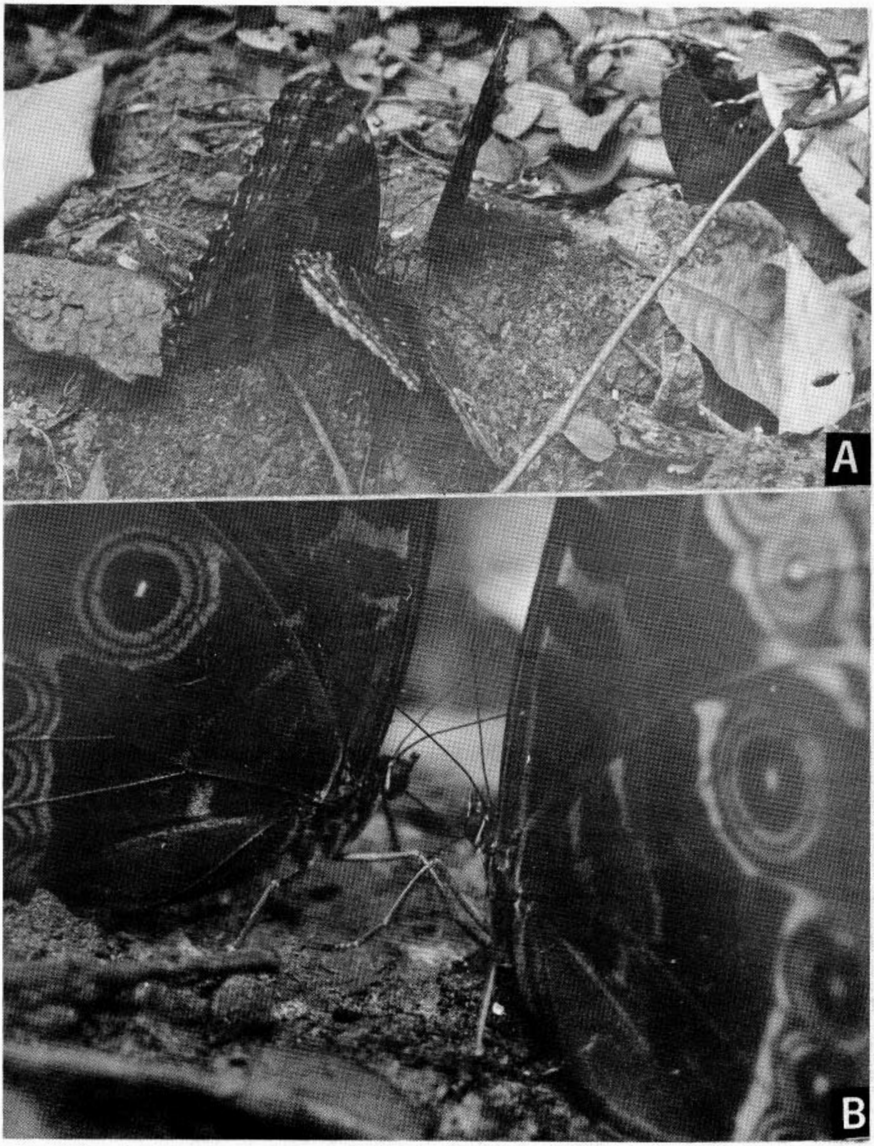

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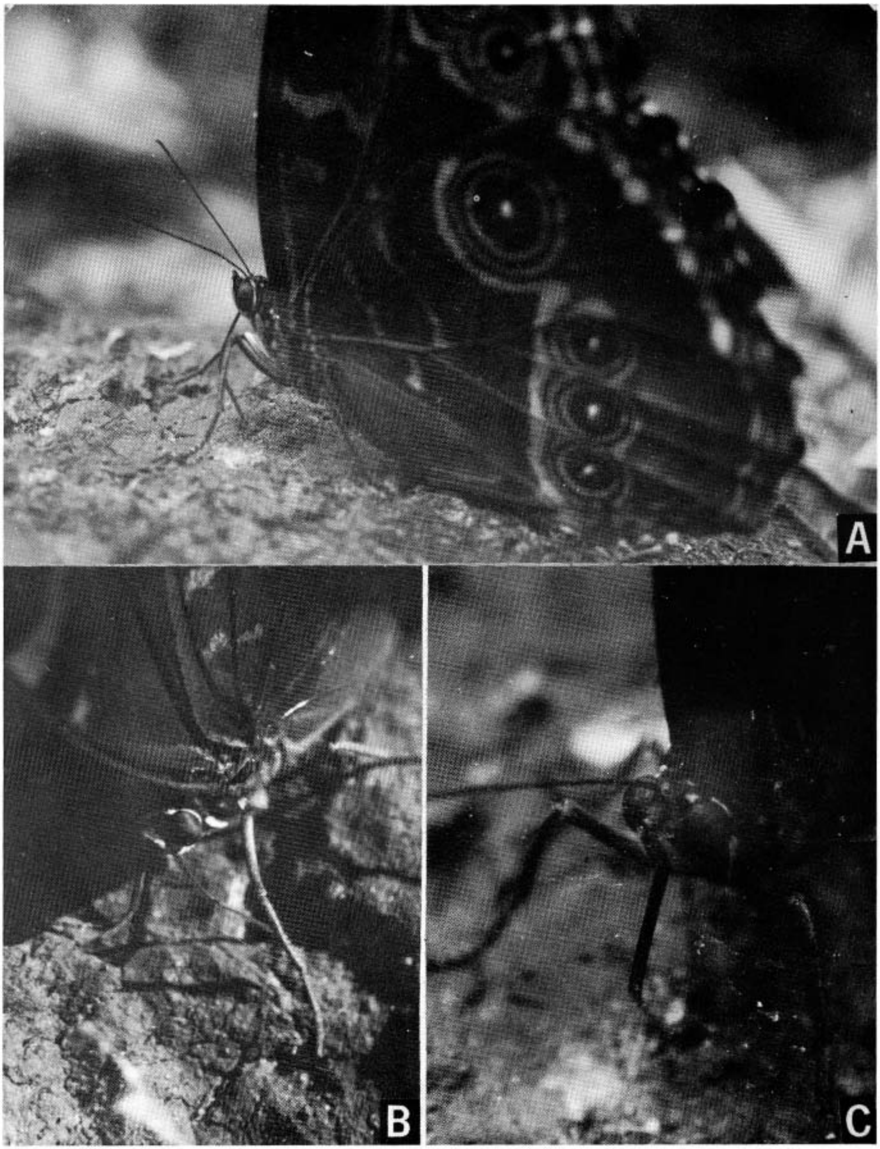
Fig. 5 A. Note the proboscis of this feeding individual: it is touching the left side of the small white area (feeding site) on the root. B. close-up view of feeding: note the proboscis. C. the proboscis of this individual is on the sap flow (white area), (December 22, 1973).



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