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## NOTES ON GREGARIOUS ROOSTING IN TROPICAL BUTTERFLIES OF THE GENUS *MORPHO*

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Recent literature on general theories in community ecology has stressed the evolution of highly specialized patterns of behavior in species that inhabit tropical rain forests, (Margalef 1968; Miller 1969; Slobodkin and Sanders 1969). It is held that the stable (e.g., Levins 1968) or predictable nature (e.g., Levins and MacArthur 1967; Slobodkin and Sanders, 1969) of the physical environment in the tropics allows for organisms to cue in on the subtle features of the habitat, and adjust very well by developing very specialized and highly evolved patterns of behavior related to survivorship in low-density populations.

Clearly, studies of behavioral patterns associated with reproduction, survivorship, and daily activity patterns in natural populations of tropical organisms are needed to assess the generality of such theoretical considerations. This present paper summarizes observations on repeated gregarious nocturnal roosting in the tropical butterflies, Morpho amathonte centralis and Morpho granadensis polybaptus (Lepidoptera: Morphinae). The observed consistency and duration of this behavior in males of these large butterflies indicates that it may have selective value with respect to (1) efficient exploitation of food sources and (2) reservation of the bulk of daily energy budgets for courtship activities. With the recent exception of a discovery of this phenomenon in a supposedly tasteful nymphaline, Marpesia bernia, (Emmel and Benson 1971), gregarious nocturnal roosting habits were known mainly in distasteful species of tropical butterflies (e.g., Poulton 1930; Carpenter 1933; Crane 1955; 1957; Owen and Chanter 1969) with the adaptive value of such behavior being that the noxious or distasteful qualities of the butterflies en masse is a much more effective predator-deterring behavior than if individuals roosted singly

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(Crane 1955). The study of Emmel and Benson (1971) and the present paper suggests that different species of tropical butterflies, both distasteful and tasteful forms, have evolved such behavior as different adaptive strategies. Unlike the interpretation of such behavior in other butterflies (e.g., Emmel and Benson 1971), it is unlikely that gregarious roosting in *Morpho* butterflies acts as a mechanism against predatory attacks.

#### Observations

Four roosts of adult male Morpho amathonte were discovered during January and early February 1970 in a lowland tropical rain forest ("La Selva") located in northeastern Costa Rica. These discoveries were made in conjunction with observations on the feeding and flying activities of these butterflies, and these studies are summarized elsewhere (Young 1971a). All of the butterflies seen at each roost turned out to be those that had been marked previously at their daily feeding sites (natural accumulations of fallen fruits of the canopy tree. Coumarouna (= Diptyerx)oleifera (Papilionaceae—"Almendro"); the group of butterflies associated with a feeding site were the *same* individuals that roosted together during the night. There was no exchange of individuals among the widelyseparated four feeding sites studied and observations were made to determine the extent of roost faithfulness, in addition to survivorship and recruitment rates. At the time of discovery of these roosts, they consisted of 5, 2, 2 and 5 individuals (with the order being roosts 1, 2, 3 and 4 to correspond with feeding sites 1, 2, 3 and 4 discussed in Young 1971a).

One roost of adult male *Morpho granadensis* was discovered during May 1970 in the montane tropical rain forest located near Cuesta Angel in central Costa Rica. This roost initially consisted of 14 individuals and over a 10-day period, all of these butterflies were marked in order to determine roost faithfulness, survivorship, and recruitment rates. Unlike *Morpho amathonte*, these individuals were not marked at their feeding sites since these were not known. However, at La Selva, a few individuals of this species were seen roosting with *Morpho amathonte* and these butterflies were also observed. Marking was facilitated in this species as they were easily netted after 5 PM (CST). In both species, an enamel base paint, "Flo-Paque," was used to mark butterflies; each butterfly was given 2 distinct markings on the undersides of the wings: one mark to denote roosting site, and another mark to denote individual number.

The four roosts of *Morpho amathonte* were observed for five consecutive months, with observations being made on several days per month. The roost of *Morpho granadensis* was observed for 3.5 months and not as frequently as those of *Morpho amathonte*. At the time of marking, the wing condition of individuals (tattering, loss of scales, fading) was noted in order to study changes in the age-structure of the adult population; sex was also determined. The latter was easily done since males are much brighter and possess different markings than females, and thus sexes could be distinguished at a distance.

In the case of *Morpho amathonte*, all four roosts were situated in low, open, secondary-growth vegetation encompassed by closed-canopy forest. These roosting sites were very close to feeding sites and typically no more than 35 meters away. Adults usually roosted on the upper surfaces of large-sized leaves of various plant species, and in vertical positions. Wings were always kept tightly closed while roosting, and against the background of dark green foliage and shadows, the butterflies were difficult to see even at close distances. Adults were widely spaced with the nearest distance between two individuals being a few feet. It was never seen that more than one adult rested on a leaf; perhaps in this respect roosts of Morpho butterflies are structurally different than those of other species. Emmel and Benson (1971) report on the occurrence of several individuals of Marpesia bernia roosting together on the undersides of a leaf. Undoubtedly size of the insect is an important factor in determining the relative proximity of individuals in a roost; Morpho butterflies are very large (average wingspan 25.5 cm in both species) and perhaps require more space on a per individual basis. Furthermore, adult males are aggressive along their flight paths (Young 1971a) and this may be an important factor in determining the distances among roosting individuals. Aggressive interactions among males at roosting sites have not been observed.

The roost of adult male *Morpho granadensis* was located on branches of trees that were overhanging a river (Rio Sarapiqui) and individuals hanged from the upper surfaces of leaves. Whereas the roosts of *Morpho amathonte* took on a more circular configuration due to the shape of the openings in the forest used, the roost of *Morpho granadensis* was oblong in shape in that it extended along the river bank and included various species of trees. However, individuals were again widely-separated. Individuals roosted about 1.5 meters above the water and in the case of *Morpho amathonte*, individuals roosted from 2 to 5 meters above the ground. In two of the roosts of *Morpho amathonte*, individuals of *Morpho granadensis* were seen over long periods of time. At one roost (roost 2) there were 3 individuals of *Morpho granadensis*, and at a second roost (roost 4) there were 2 individuals. Like the Cuesta Angel roost, all of these individuals were males.

A summary of the temporal patterns of roost occupancy are given in Table 1. As seen for adult aggregations at feeding sites (Young 1971a), there was virtually no turnover in adult males of *Morpho amathonte* at

				Number <sup>c</sup> of Butterflies		
Months	$N^{b}$	Locality	Roost No.	Females	Males	Total
Morpho amathonte						
Feb. Mar. Apr.	$14\\20\\18$	La Selva	1	0 0 0	5 5 6	5 5 6
May June <sup>d</sup>	22 5			0 0	65	65
Feb. Mar. Apr. May June <sup>a</sup>	$14 \\ 20 \\ 15 \\ 20 \\ 6$	La Selva	2	0 0 0 0 0	2 2 3 3 2	2 2 3 3 2
Feb. Mar. Apr. May June <sup>a</sup>	$14 \\ 18 \\ 17 \\ 19 \\ 5$	La Selva	3	0 0 0 0 0	2 2 2 2 2	2 2 2 2 2
Feb. Mar. Apr. May June <sup>d</sup>	$13 \\ 20 \\ 18 \\ 20 \\ 5$	La Selva	4	0 0 0 0 0	5 5 6 5	5 5 6 5 5
		Morpho gi	ranadensis			
Apr. May June July <sup>a</sup>	8 11 17 8	Cuesta Angel	1	0 2 0 1	14 16° 10 13°	$14 \\ 18 \\ 10 \\ 14$

TABLE 1. Evidence for high roost faithfulness<sup>a</sup> in adult Morpho butterflies in Costa Rican tropical rain forests.

a Defined here as the continuous occupancy of the same roosting site(s) over a long period of

<sup>a</sup> Defined nere as the continuous occupancy of the same roosing she(s) over a roos period of time (several months). <sup>b</sup> N is the number of days of observation at roots each month. <sup>c</sup> These are means; standard errors were very small and are not included in the table. <sup>d</sup> For Morpho amathonte, there was only one week of observation during early June; for Morpho granadensis, there was only 8 days of observation during early July. <sup>c</sup> Increments in adults numbers was due to appearances of newly-emerged males at the roost.

their nocturnal roosts. Turnover was more prevalent with Morpho granadensis (Table 1).

The time of departure and arrival of the butterflies at the roosts each day was highly variable and depended upon local weather conditions. This was particularly true for Morpho granadensis. On overcast afternoons, individuals arrived usually between 4-6 PM, whereas on sunny afternoons, arrival was usually restricted to 5:30 to 6:15 pm. It is of interest to describe the pattern of arrival of individuals at the Cuesta Angel roost of *Morpho granadensis*. The roost was located along a river bank at

the base of a steep gorge covered with closed-canopy tropical rain forest. Standing on the opposite of the river and directly in front of the roost site. with the aid of binoculars, the pattern of arrival could easily be observed for these very large and conspicuous butterflies. On all days of observation (a total of 54), the arrival pattern was the same and fascinating: one by one, and following each other at very close intervals, the butterflies would lazily fly down to the roost from the upper reaches of the gorge. They formed an imaginary line of blue objects as they flew down the gorge over the tops of the trees. They always approached the roost from one side and several meters away; then they would fly along the river bank until they reached the roost. On a sunny day, all individuals were in the roost within 25 minutes; the time involved was longer on overcast days but the pattern was the same. By being stationed very close to the roost, it was possible to observe the actual order (of marked individuals) of arrivals; this pattern was highly variable each day. Departure occurred usually between 8:30–9:30 AM each day and individuals flew off in different directions. In Morpho amathonte, arrival was staggered and individuals flew in from different directions. Departure was of a similar pattern and the roosts were usually vacated by 7:00 AM each day. No consistent order of arrival and departure for the marked individuals of this species could be determined. Young (1971a) suggests that adult males of this species elect to roost overnight in open, exposed areas in the forest so that they may receive the early sun ray to assist their bodies becoming sufficiently warmed-up for flight. This in turn, is related to the diurnal activity pattern of this species: adult males feed from 7-8:30 AM, fly on consistent flight paths from about 8:30 AM to 11:30 AM, and either partake in courtship activity along flight paths beyond this hour or rest near feeding sites before moving to nocturnal roosts between 5:00 and 6:00 PM (Young 1971a). Under such a diurnal activity pattern, it is expected that arrivals at roosts would be inconsistent, depending upon whether individuals were involved in courtship or resting near feeding sites.

On the other hand, both adult male and females of *Morpho granadensis* concentrate the bulk of their feeding activity to the late afternoon hours (3:00–6:00 PM) and presumably engage in courtship activity earlier in the day (Young 1971b). Like *Morpho amathonte*, adults of *Morpho granadensis* aggregate at feeding sites (at La Selva, these can be the same ones used by *Morpho amathonte*) (Young 1971b). The cessation of feeding with advancing nightfall or undesirable weather conditions may account for the "group return" pattern of arrivals to roosts in this species; since all individuals are involved in the same activity and at the same time, it is expected that they would be more consistent in arriving at roosts.

While it is clear that there is no movement of individuals once they are

settled in roosts, if a roost is approached (by human observer) to within about 2 meters of a resting individual, that individual will fly away for a short distance. When the disturbance is stopped, the butterfly will return to its original perch usually within 15 minutes. Depending on the direction of flight upon disturbance, an individual can either cause other resting individuals to fly or else there is no effect at all on other members of the roost. When branches were marked with small pieces of brightly-colored tape, it was discovered that individual butterflies in a roost almost always return to the same tree each day for nocturnal roosting. Such specificity for a given roosting site may imply the use of scent that is laid down and reinforced on subsequent visits. The problem, however, is very complex since individuals in a small area can single out their own roosting spots on different days. Wilson (1968) and Regnier and Law (1968) state that it is quite possible for different individuals of a species to possess individual-specific pheromones, resulting from subtle genetic differences, diet differences or other factors in the environment. Chain-reaction effects, in which one disturbed individual could initiate flight activity in other individuals were generally uncommon, although they occasionally occur. Unlike other known cases of roosting butterflies (e.g., Emmel and Benson 1971; Clench 1970), due to the relatively large distances among members of a roost in Morpho, it is unlikely that mass flight can result from disturbance directed to a single individual.

#### Discussion

Adult male butterflies of Morpho amathonte and Morpho granadensis form sleeping roosts of low densities in tropical rain forests. The low densities of members in these roosts is related to the adult population structure in these butterflies; adult male populations of Morpho amathonte are very small and individuals maintain the same individual-specific flight paths in the habitat. This is probably true for adult Morpho granadensis. Aggressive interactions occur along these flight paths and courtship behavior has also been observed on them (Young 1971a), and it is suspected that these flight paths function as territories. Flight paths radiate out from feeding sites, accumulations of decaying odorous fruit on the forest floor. Males from roosting aggregations very close to where they feed and both feeding sites and roosting sites are maintained over long periods of time. When the feeding site becomes non-functional (with cessation of fruit-fall), the butterflies disappear and the roosting sites become unoccupied. It thus appears that in Morpho amathonte, the location and usage of a roosting site is dependent primarily upon location and usage of a feeding site. Less is known about the relation of feeding sites and roosting sites in Morpho granadensis, although roosts are apparently used for long

periods of time. Thus, rather than a roosting site being used throughout the lifespan of individual adult males, occupancy depends mainly on persistence of feeding sites. Adult *Morpho* butterflies have been estimated to live close to 9 months (Young 1971a) and the maximum period of exploitation of certain feeding sites (and thus roosting sites) is 5 months.

The high turnover of adult males in the roost of *Morpho granadensis* may be interpreted as the result of predation on adults counterbalanced by low, but continuous recruitment of newly-emerged adults. In populations of *Morpho amathonte*, there is very little recruitment of adults at feeding sites and there is virtually no mortality of adults from predation (Young 1971a); thus, numbers in roosts tend to remain the same.

Young (1971c) advances a novel hypothesis to account for the differential predation by birds on species of butterflies belonging to the genus Morpho. Under this hypothesis, the apparently high mortality of adults in Morpho granadensis from predation is explained by the lack of an effective predator-deterring behavior pattern that is very effective in adult male populations of *Morpho amathonte*; adults of the latter species are successful at escaping from avian predators by attracting them through marked changes in flight behavior and then frustrating them in relatively short time. That adult Morpho butterflies are tasteful to avian predators is shown by (1) the discovery of wing fragments (bearing beak-marks) of certain species (Morpho granadensis and Morpho peleides) on the forest floor, under bird perches, (2) observations of attempted attacks by birds in the field, and (3) records of larval food plants apparently exclude genera known to contain noxious compounds that make other species distasteful (Ehrlich and Raven 1965). Larvae of Morpho peleides, a species closely related to Morpho granadensis (both are in the achilles group), in El Salvador feed on leaves of Machaerium riparium in the Leguminoseae (Alberto Muyshondt, V. E. Rudd, personal communications); the Leguminoseae are not known for toxic or noxious compounds. Not only are the present observations a first record of gregarious roosting in Morpho butterflies, but it is apparently the second recorded case of a palatable species showing such behavior, as the report of Emmel and Benson (1971) constitutes the first record for a palatable nymphaline. It is well known that many species of palatable butterflies are readily taken as food by caged birds (e.g., Brower and Brower 1964), but less known is the relationship between palatability and gregarious behavior in tropical butterflies.

Low turnover of adults, in addition to being related to levels of predation, may be due to a very long developmental time in these butterflies; for an undetermined species of *Morpho* in El Salvador, the developmental time from egg to adult under natural conditions is over 2 months (Senor Alberto Muyshondt, personal communication). One recent study (Young 1971d) indicated that several species of tropical butterflies belonging to various genera have very long developmental times. Long developmental time, low adult population density, and mortality (predation and parasitism) on both adults and immatures may account for the low turnover of adults in *Morpho* populations (Young 1971a).

The lack of adult females from the roosts of *Morpho* butterflies may be due to undesirable behavioral interactions with males that could occur there. For Morpho amathonte, it is known that females are relatively rare at feeding sites where males aggregate, and when they feed there, they do so when males are absent (Young 1971a). Less is known about the behavior of adult females of Morpho granadensis. Interactions between sexes do not occur at feeding sites nor at roosting sites in either species: in Morpho amathonte, courtship takes place along the flight paths of males (Young 1971a). Causal observations at La Selva suggest that adult females of Morpho granadensis sleep singly on understory vegetation in the forest; specific locations for sleeping females are highly variable and the same spot is used for only a few days. Adult females of both species are probably much more variable in their daily behavior than are males. Females must continually search for suitable oviposition sites and since they are probably very long-lived (since males are), they probably remain fecund throughout the bulk of adult life and this implies a continual search for oviposition sites. Such a characteristic of their biology, obviously not shared by males, may account for the lack of similar predictive behavior in them. Data on the spatial distribution of immatures and how it relates to the spatial distribution of larval food plants are needed in order to understand behavior of females in Morpho butterflies.

The absence of females from roosts of males may also be an indication of a behavioral mechanism that prevents sexual interactions to occur in places in the habitat where several males may be present at the same time. The absence of females from nocturnal roosts as well as from feeding sites of males may prevent severe aggressive interactions that would result in failure of females to be mated; courtship interactions would be more successful in aggressive species at places where the chance of multiplemale encounter would be low. However, such behavior implies that adult males must have a very effective patrol behavior pattern for females in such low density populations; this is apparently the case for at least *Morpho amathonte* (Young 1971a).

Independent of any gregarious property of roosting in tropical butterflies, protection to individual members of a roost may result from the positions of perching. For example, Emmel and Benson (1971) interpret the perching of roosting *Marpesia bernia*, a tropical nymphaline, on the undersides of leaves as a means of shielding individuals from both rain and the view of potential avain predators. In the same species, roosting near the tips of branches may ensure protection against roaming, leafgleaning insectivorous predators such as ants. The roosting of *Morpho* butterflies with their wings tightly closed (showing the cryptic undersides) and in vertical positions on the upper surfaces of leaves and near the tips of branches may also give protection to individual butterflies from rain and predators. At the time of day when the butterflies arrive at their roosts, they are very difficult to see when resting (protection against birds), and their positions on the outer surfaces of hanging leaves gives them a lot of room to leap out when disturbed (e.g., upon approach of a leafgleaning predator). During heavy rains, I have witnessed various roosting individuals to go practically untouched by rain resulting largely from their vertical positions with the wings kept tightly closed.

The repeated occupancy of the same roosting site by the same individuals over long periods of time suggests that these butterflies have evolved an efficient means of becoming very familiar with a portion of their habitat-e.g., it is a form of predictable behavior which such specialized behavior is related to protection resulting from coordinated group activity is not clear. The lack of close proximity of roosting individuals at a given roost does not allow for any one individual to "warn" the remaining members of the aggregation of an approaching danger (predator), and thus it is very unlikely that gregarious roosting in *Morpho* butterflies provides some protection to the group from predation. Rather, it appears that this behavior is the result of the butterflies aggregating at their feeding sites, which are very close by (at least for *Morpho amathonte*). Field observations support the view that all individuals simultaneously present at a feeding site will fly away when a human observer walks through the area (Young 1971a), even though different individuals may be widely separated. At feeding sites, gregarious feeding of Morpho butterflies appears to act as a behavioral mechanism against predatory attacks by resulting in chain-reaction effects of butterflies flying away. Depending on the proximity and number of potential nocturnal roosting sites that provide exposure to morning sunlight, there is a reasonable probability that several or all adults (since numbers are generally low per feeding site) associated with a given feeding site will actually roost in the same open spot in the forest. And as pointed out for certain pierid butterflies (Clench 1970), the presence of one individual at a roost may attract others to it; such an attraction, in the case of Morpho, may involve both chemical stimuli and visual cues. Tethered live individuals or paper models can attract other living individuals (Young 1971a). It thus may be very efficient for all individuals associated with a given feeding site to select, independently

of each other, the closest suitable nocturnal roosting site, so that very little energy has to be expended in traveling to feeding sites. Such a strategy appears feasible for at least *Morpho amathonte*, since adult males of this species spend a great amount of energy patrolling well-defined flight paths in search for mates (Young 1971a) and since a great deal of time and energy is put into such reproductive activities, less energy is available to search for new feeding and new roosting sites on a short-term (e.g., day-to-day) basis. The exploitation of the same feeding sites and roosting sites on a daily basis allows adult males to partition the bulk of their energy supply into territorial flying in search of mates.

While similar data are lacking for the daily activity schedule of adult males of *Morpho granadensis*, it may be that similar behavior patterns are present; i.e., the bulk of energy supply is channeled into activities associated with reproduction and only minimal amounts are used in the selection of feeding and roosting sites.

Such strategies appear to be of great evolutionary and adaptive significance in tropical organisms since population density is generally low in species that comprise tropical rain forest communities (e.g., Margalef 1968) and under such conditions of low density, a premium is placed upon highly specialized behavioral patterns that ensure courtship encounters. Thus, rather than gregarious roosting in Morpho butterflies having selective value in terms of predation, a more likely hypothesis, based on the structure of the roosts and their relation to feeding sites, is that they are a part of the predictable and efficient overall behavior of these butterflies that allow for the bulk of the daily energy budget of males to be used for courtship encounters. The closer spatially that feeding sites and roosting sites are to one another, the less energy is required to fly between them. Nocturnal roosting at feeding sites is presumably undesirable in that these areas are usually well-shaded from morning sunlight; roosting in an area exposed to morning sunlight ensures early activation of the butterflies. For Morpho amathonte, this behavior ensures early arrival at feeding sites before territorial flying; for Morpho granadensis, although data are lacking, such behavior may ensure initiation of searches to seek mates, since the bulk of feeding in this species occurs during late afternoon hours and presumably the food intake on a given day is put into use the following morning with courtship activities.

#### Summary

Observations were made on gregarious, nocturnal roosting by adult males of the large, tropical butterflies, *Morpho amathonte centralis* and *Morpho granadensis polybaptus* at two different sites in Costa Rican tropical rain forests. Individuals of these species roost gregariously in that several individuals sleep in the same open area in the forest, although they are close to one another. High fidelity to roost is indicated by occupance over long periods of time (several months) and turnover of adults is usually low. Interactions (e.g., aggressiveness) among males does not occur at roosting sites and females are rare. Although not entirely ruled out, it is difficult to conceive of such behavior in males of these butterflies as being a form of collective defense against predators. A more plausible explanation, based on data on daily activity schedule including feeding and flying activities for *Morpho amathonte*, is that such behavior is a byproduct of the gregarious feeding in these butterflies since feeding sites are located very near roosting sites. As with roosting sites, there is high fidelity by adult males of *Morpho amathonte* for feeding sites. Independent of the gregarious aspect of this roosting behavior, the type of position that the butterflies use may give protection against heavy rain and predators.

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## TWO MOSAIC GYNANDROMORPHS OF AUTOMERIS IO (SATURNIIDAE)

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The recognition of a gynandromorph in nature is an exceedingly rare event. Hessel (1964) described a bilateral gynandromorph of Automeris io Fabricius taken at Washington, Connecticut. He refers to the capture of bilateral gynandromorphs of Eacles imperalis Drury taken at Pottersville, N. J. (1962) and Callosamia promethea taken at Crown Point, Indiana (1962) as momentous events in light of the extensively collected Saturniidae. The appearance of two gynandromorphs in a single season is unusual, and the data provided by these specimens is extremely valuable in understanding gene action.

In most Lepidoptera the female is heterogametic. Doncaster (1914), Remington (1954), and others have shown the female to have either a pair of non-homologous sex chromosomes (ZW type) or that one chromosome will be lacking (ZO type). The male possesses a homologous pair (ZZ type).

In A. io. the northern populations are polymorphic; the basic color of

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