Studies on the ecology of Ithomiinae and Heliconiinae in Costa Rica[1]

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ABSTRACT

Several aspects of the ecology of Ithomiinae and Heliconiinae in Costa Rica are discussed. Behavior of *Mechanitis lycidice* was studied and a dry-season time budget established for the population. Comparisons were made between species' behavior and the patterns of mortality in eggs, larvae, and pupae of several heliconiines. Behavior is predator rather than competition oriented and predator induced mortality is the major population regulating factor. Comparisons were made between roost fidelity of *Heliconius erato* and *Dryadula phaetusa*. Morph frequencies in a polychromatic population of *Heliconius doris* at Rincon, Osa Peninsula, Costa Rica were determined and a possible selective mechanism proposed for the maintainance of the system.

INTRODUCTION

Following from the classical publications of Bates (1862) and Müller (1879), there has been much effort expended on mimetic theory. Until recently, most studies were comparisons of museum specimens and spotty observations; mimicry was treated as a static condition rather than a dynamic process. Static approaches obviate the necessity of ecological data and knowledge of the systems in nature or their evolution. The analytic evaluation of selective mimicry was set on a firm foundation by Fisher (1958) in 1927, but only recently has this approach been pursued using mechanistic principles with supporting experimental data (Holling 1965, Huheey 1964, Brower *et al* 1964a).

Heliconiine and ithomiine butterflies have contributed the most important examples of mimicry in the Neotropics. Ecological and behavioral data are rare for most groups of Lepidoptera, although some heliconiines have been the subject of considerable study. These include larval and pupal behavior (Alexander 1961a, 1961b), imaginal

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behavior (Crane 1955, 1957), relative palatability (Brower *et al.* 1963, 1964b), and genetics of geographic and polychromatic forms (Turner and Crane 1962, Sheppard 1963, Emsley 1964). The Heliconiinae were revised by Emsley (1963, 1965) and the Ithomiinae partially revised by Fox (1956, 1960). Further, there are many abundant species in moist warm regions of the American tropics, many being low flying and accessible to observation.

Many Heliconiinae and Ithomiinae participate in specific mimicry complexes, but the precise selective pressures that maintain these systems are poorly known. Through a knowledge of the regulatory and selective forces impinging on the various species and how population behavior relates to the systems, we can better understand mimicry as an ecological and evolutionary process.

This study involved examining several processes in the ecology of ithomiine and heliconiine butterflies. Individual aspects are presented and discussed separately. The diversity described should demonstrate the interactive possibilities of distasteful butterflies in mimicry complexes.

HELICONIINAE AND ITHOMIINAE OF COSTA RICA

Of the 55 described species and 7 genera in the subfamily Heliconiinae, 25 species and 6 genera are known from Costa Rica. This includes the monotypic genera *Dryadula*, *Dryas*, *Agraulis*, and *Philaethria*, two of the three species of *Dione*, and 19 of the 45 species of *Heliconius*. Only *Podotricha* is absent from Costa Rica. These 25 species can be broadly divided into ten groups on the basis of color pattern of which five possess patterns shared with other species of Lepidoptera in Costa Rica. A similar comparison was not attempted for the Ithomiinae since a compilation including all of the Costa Rican species is not available (Table I).

Distributional data were obtained for the heliconiines from three localities in Costa Rica during February and March, 1967. These included a tropical moist forest area 8.5 mi. southwest of Cañas in Guanacaste Province, a tropical wet forest area near Rincon, Osa penninsula, Puntarenas Province, and a sub-tropical wet forest area 3.5 mi. south of San Vito, Puntarenas Province. The observations were made near the middle of the dry season, and each sample was taken over a two to three week interval.

The heliconiines are primarily inhabitants of moist areas, often seasonally, with 12 or 14 species being observed at each of the wet sites and three at the dry site. Two of the three species at Guanacaste constituted three individuals and were restricted to an area along the Rio Higueron. A similar pattern was noted with the ithomiines, with two species from the drier area and approximately twenty from each of the wet areas. The distribution of these species is probably correlated with food plant distributions, with physiological tolerances superimposed (Table II).

TIME BUDGET OF MECHANITIS LYCIDICE

Mechanitis lycidice is a common butterfly of low and intermediate elevations in Costa Rica and usually occurs in the deep shade of primary and old second growth areas, especially along stream banks. In areas with severe dry seasons, it seems restricted to river-bottom forests. The wing pattern of M. lycidice is extremely variable, and two extreme forms of a continuously varying population have been recorded by Seitz (1924) from Costa Rica. Form M. l. lycidice is reported to range from Hondurus to Costa Rica and form M. l. isthmia from Costa Rica to Panama, the M. l. lycidice form predominating in northern Costa Rica and M. l. isthmia predominating in the south.

A highly variable population of M. lycidice in the river bottom forest along the Rio Higueron, Finca Jimenez, near Canas was studied from February 7 to February 19, 1967. The dry season begins in December and extends to late March at this locality. The highest population density was recorded in an area approximately 200 m long and 100 m wide, paralleling the Rio Higueron, 300-400 m to the west.

Behavior of the sexes was not recorded separately since they are indistinguishable in flight and at rest. Wing lengths of 41 males and 38 females yielded means and ranges of 33.6 ± 4.6 mm and 35.6 ± 5.6 mm, respectively. The sex ratio was not significantly different. Observing individuals whose sex was determined was not attempted because of the well developed alarm reaction upon release and other possible atypical behavior.

An attempt was made to determine population size with a mark-and-recapture procedure. Red and green "Marks-A-Lot" felt-tip marking pens were used to mark the underside of the wings of 74 individuals, using the method of Ehrlich and Davidson (1960). Thirty-three individuals were marked and released on Feb. 8, eighteen on Feb. 13, and twenty-three on Feb. 17, 1967. On February 18, 1967 thirty butterflies were removed from the population, of which two were recaptures. The calculated population estimate was 1110 individuals; however, this is of low reliability because of the small sample of recaptures involved. It is also possible that immigration to and from the population and differential mortality of marked individuals may have placed this value much above the true population size.

The predominant behavior patterns recorded in the time budget were sitting on foliage, flying, and chasing of butterflies of the same species. The latter occurred so rarely that no systematic attempt was made to determine its frequency or temporal importance. The time spent sitting and flying was determined by two different methods. Method I was recording the time spent sitting by a newly settling butterfly and then recording the flying time when it is moving to another position. Method II was recording the total flying time in a delimited area where the butterflies were abundant. At the termination of the observations the number of butterflies in the area was censused. Method I is biased in that some of the butterflies flew beyond the range of vision and others continued to rest when the observation was terminated 30-45 minutes later. Bias occurs in Method II in that the butterfly density at the end of the observation period was not necessarily the mean density for that period and, since the density was relatively high in the area, more flying than usual may have been observed owing to mutual disturbance of individuals. These observations indicate that 0.68-3.36 % of the population time in Mechanitis lycidice is spent flying and the remainder spent sitting on leaves (Table III).

The time spent resting is usually in association with other individuals of the same species. This was demonstrated by walking through the study area and recording the number of individuals frightened into flight simultaneously. Flying individuals were not strikingly associated with other individuals of the same species (Table IV).

Earlier in the morning, sitting butterflies tended to be higher on the vegetation than later in the morning and through the afternoon. This is substantiated by observational data showing that prior to 0830 the butterflies average about 1 m above the forest floor when resting, while after this time the mean is near 15 cm (Fig. 1). This is probably associated with mating behavior since all of the chasing behavior that was observed occurred during the earlier part of the morning. It should be noted, however, that the females were in reproductive diapause (O. R. Taylor, personal communication).

The following behavior patterns were looked for but not observed: feeding, flower visiting, copulation, ovipositing, and gregarious sleeping.

Flying in the same area at lower frequency (six males were captured in the area) was Tithorea harmonia helicaon. This butterfly is very similar to the lycidice form of Mechanitis lycidice and was not usually separable from M. lycidice when in flight. These ithomiine species may provisionally be considered Mullerian mimics until experimental data are available.

HELICONIINE EGGS, LARVAE, AND PUPAE

The factors that regulate population sizes in distasteful butterflies, as with most insects, are largely unknown. With adult stages that are highly protected from vertebrate predators, other factors must be acting to limit population sizes.

Eggs in three species of heliconiines were observed in situ. Ovipositing sites were relatively constant in each species. Two species are known to oviposit on Passiflora vitifolia at Rincon. One deposits a white or buff-yellow egg on or near the apex of fully formed free tendrils (5 eggs) or less commonly on the underside of a new leaf on the shoot tip (1 egg). Of the five eggs observed under natural conditions, three desiccated apparently from radiation, the one on the terminal leaf was found frayed (perhaps from ant predation), and observations were terminated before the fate of the remaining egg was determined. All eggs were located on perdant vines between 1 and 1.5 m above ground level. No egg was kept under observation for longer than 24 hrs.

The second species ovipositing on Passiflora vitifolia deposited clusters of approximately 80-160 reddish eggs on the undersides of fully expanded leaves. The eggs are arranged in parallel rows up to 2 cm long and 1 mm apart, and the eggs are spaced at 1 mm intervals in the rows. The cluster may measure 2.0 x 2.5 cm. Three egg clusters were found; two were on the third from terminal expanded leaf and the remaining on the fifth from terminal. All were on pendant vine branches 2.0 to 2.5 m above ground level. One cluster was intermittently observed over 34 hrs with only a change in egg color to maroon six hours before the eggs hatched.

The third species oviposited on Tetrastylis lobata (Passifloraceae) at San Vito. Two ovipositibn sites wdre found on the underside of terminal leaves, ove with a single egg and the other with three. The heights above ground were 1 and 0.1 m, respectively. These eggs were observed for two days with no changes recorded.

The oviposition sites and distances above ground level for the two species that presumably feed on P. vitifolia suggest a possible division of food resources. These sides may also be influenced by predation since lower stems are more accessible to ground-dwelling predators. The species laying fewer eggs at one site or with less aggressive larvae might find it better to start their larvae on lower vines as single individuals and chance predation rather than on higher vines where competition could occur with the species laying clusters of eggs.

A number of Passifloraceae are known to produce cyanogenic glycosides and harmine alkaloids (Brower et al. 1964b) that could serve to limit consumption rates even by adapted predators or be produced in larger quantities at wound sites. Other mechanisms are available in the form of petiolar and foliar nectaries that seem to serve as attractants to insects, particularly predaceous ants. Ants of the genera Camponotus and Ectatomma have been seen visiting the in that foraging on the vine was undirected, predation occurring only when an ant chanced to come across a larva or larval group. Upon finding larvae an ant would crouch on its metathoracic legs, pivot froward, and lunge. Often two or three larvae were picked up in this manner. If more larvae were present and the mandibles not too full, the process was often repeated. Although no specific response was noted of the larvae in the presence of an ant, mild contact often elicited head rearing. When grasped by an ant away from the head, the larvae would swing in a "J", bringing the head close to the point of irritation. Noxious salivary or gut secretions may also be present since ants with larvae grasped in this way appeared to undergo mandibular and head wiping more frequently. The complete sequence involved an attack, backing off with larvae, stinging, head and mandible wiping, and carrying off of the prey. Both stinging and wiping were occasionally omitted, often inexplicably. In one aberrant case an ant grabbed, backed off, and cleaned from its mandibles a mass of smaller larvae three times in succession. It is apparent that these heliconiine larvae are not ideal food for Ectatomma. tuberculatum Ol.

The functioning of the larval aggregation as a protective mechanism is not obvious from these observations; however, it is possible that removal would be faster in isolated larvae. If the larvae were larger or the predator smaller, the group defense might have been more effective.

Despite the heavy mortality observed in both eggs and larvae, competition for food could still be an important factor in the ecology of these insects. The number of predator-free oviposition sites is no doubt low, and larval interactions here could be very important. At this time there is no way to know to what degree the imaginal populations are recruited from larvae that have escaped predation or that have survived competition.

At San Vito the Tetrastylis vines appeared to be free of ants. Heliconiine larvae of one species were present in all stages on the plants, with up to three individuals on a branch. No interactions were observed between these larvae even when only millimeters apart. If this behavior can be used as a criterion, it would seem that competition for food in the larvae of this species is not important. Oviposition behavior of the adult may be a more efficient mechanism in circumventing competitive interactions.

Although systematic observations were not made on the Tetrastylis-inhabiting larvae, some of their behavior patterns are of note. First and perhaps second instar larvae remained on the temdrils and terminal leaves through the night and early morning hours. An early first instar larva was also observed feeding on a pendant tendril. Both of these processes could serve to reduce predation, the former by making the larvae less accessible to stem and leaf foragers and the latter by killing and preventing the tendril from entangling another plant that might open a pathway to predators.

Violent head thrashing was observed in a 4^{th} or 5^{th} instar larva in response to a fly hovering above it; the behavior continued for 15 sec before the dipteran flew away. This behavior is of importance nectaries of Passiflora vitifolia and both seem to actively search the vines for prey.

Larvae from the egg clutches on P. vitifolia were observed in detail. Larvae eclosed under the third full leaf at 2100 hrs on March 10 and by 0700 hrs the following day the 150 larvae had consumed 10-15 % of the central lobe of the leaf. A second group of larvae had been under observation on the sixth leaf on the same branch since March 9 at 1015 hrs. At this time they had eaten approximately 25 % of a lateral lobe, probably having eclosed the previous evening. Between 2100 hrs on March 9 and 1400 hrs on the following day the larvae had migrated to the fifth leaf after having consumed half the surface area of the sixth.

The larvae of this species characteristically form rows of parallel individuals when feeding along the margins of the leaf. The smaller larvae (first instar) feed by epidermal scraping, while larger larvae tend to eat the entire leaf. Once epidermal feeding has begun, some larvae will feed facing invard on the leaf while standing on the remnant midrib and veins.

On March 11 the older group of larvae migrated to the fourth leaf. At 0753 hrs the group was becoming active and some individuals began to move down the lateral midrib. At 0745 hrs the trail bifurcated at the base of the leaf, one going down the petiole and another up the central midrib. By 0749 hrs the trail along the central midrib had been withdrawn and other trails formed up and down the stem and onto the tendril. Eighteen larvae remained feeding on the fifth leaf at 0753 hrs while 3 minutes later the leading larvae reached the petiole of the fourth leaf. By 0800 the feeding group was breaking up and a minor column on the other lateral lobe returning to the petiole. The larvae began to aggregate as a tight whorl under a lateral lobe of the fourth leaf at 0810 hrs with a single disjunct trail leading back to leaf five. Although the trail was discontinuous, single stragglers seemed to have little difficulty in finding the new site. Possibly each larva lays a silk strand as it moves which serves as a trail marker for following larvae. The most concentrated mass of these threads would be the path followed. At 0833 hrs the last larva had rejoined the group on leaf four, the entire migration having taken less than an hour.

The mechanism whereby a direction is decided and the function of the migration, other than finding a new feeding site, are unknown. The larvae are sub-social in the sense that the proximity of other larvae is preferred over being alone. The force responsible for this behavior would not seem to be feeding facilitation since intraspecific and intrafamilial competition for this resource should eventually become overriding. A more probable function is predator protection. This can be considered in more detail.

Ants of the genus Ectatomma were the major source of mortality in the gregarious larvae. Estimates made from differences in larval numbers through time indicate that on March 10-11 both the smaller and larger larvae were being removed at a rate of 94 to 100 individuals per 24 hrs (Fig. 2). The ants did not seem to be efficient predators in discouraging larval parasites, although Alexander (1961a) has reported similar behavior in response to loose fecal pellets, the presence of other larvae (competition ?), and general irritation.

Pupae and the remains of pupae of Agraulis vanillae were collected around P. foetida vines at Cañas to determine sources and intensity of pupal mortality. Of the seven collected, the five pupal remains bore signs of chalcid infestation and the other two contained living parasites.

It seems that the major factors limiting heliconiine populations are predation and parasitism in the immature stages. The behavior patterns evolved to cope with these factors indicate that survivors do contribute significantly to future generations and that these heliconiine populations are not merely maintained by chance survival of individuals in protected situations.

NOCTURNAL ROOSTING IN HELICONIINES

The nocturnal roosting behavior of the Rhopalocera has been little studied despite its potential importance in population biology, natural selection, and evolution. The only systematic observations known to the author are those of Crane (1957) on a number of species of heliconiines kept in insectaries in Trinidad. In the present study, roosting behavior was observed under natural conditions for several heliconiine species in Costa Rica.

At Canas, roosting was observed in Agraulis vanillae and Heliconius ethillus zuleika. A single individual of Agraulis was found roosting in a lowland pasture, suspended vertically and upside down from a grass blade. No subsequent observations were made at this location to determine if roost or area faithfulness occurred, i.e. if the same individual returned to roost at the same place or a nearby location.

Observations on roosting behavior were made on two consecutive evenings on Heliconius ethillus at Cañas. A single individual returned to and roosted over a dry water course, or run, connected with the Rio Higueron. Two individuals were originally in the area, but one was captured for identification purposes and subsequently released. This latter insect presumably left the study area. Two roosting sites were used by the remaining ethillus--the first the distal end of a dead twig on an overhanging tree (Inga sp.) and the second a dead twig or tendril associated with a hanging vine. These roosting sites were approximately 20 m apart, and both were estimated to be 5-8 m above the run.

The butterfly was absent from the area for at least one half hour prior to its pre-roosting flights. On both evenings it glided into the area through the trees on the northeast side of the run at 1711 hrs and went directly to the overhanging branches of the Inga.

This was followed by variable amounts of flying, gliding, and havering among the branches and "pacing" over the run. Several flights were made between the Inga and the immediate area of the vine before the butterfly roosted on the second evening. On the first evening, approximately 5 min were devoted to pre-roosting flight, while on the second it took 16 min for the ~~othillus~~ to roost. The butterfly landed at the apex of the projection and hung upside down, facing outwards, toward the southwest. When in this position the butterfly looked very much like a dead leaf as it swayed in the wind.

Although gregarious roosting was not observed, it cannot be excluded from normal roosting behavior since the population level at the time of the study was very low. Heliconius ~~othillus~~ does appear to be area faithful and is perhaps to some degree roost faithful in that hovering flight was observed only in a few places along the run and directly in front of the roosting sites just before roosting.

Roosting in Heliconius erato was observed over a period of four days at Rincon. The roost under observation was located 50 m above the 3-mile post on the Camino de Altura, a logging road which follows a ridge inland from Rincon. The road runs north at this point with a bank 5-8 m high to the west and a steep dropoff to the east. Second growth vegetation occupies both sides of the road except where the laterite is too steep or the bank too shaded to support growth.

The roost was very diffuse, with butterflies occupying sleeping sites spread over a distance of 125 m along the bank. The most frequently occupied roost, or main roost, consisted of the dead stalk of an annual dicot bowed out from the bank. The drooping portion of the roost was approximately 30 cm above ground level and another 10-20 cm below the level of the sheltering branches.

Another site used for roosting was located directly across from the 3-mile post and shall be referred to as the lower subroost. Here four groups of subsites were used for roosting, the first three being groups of dead twigs on the exposed underside of a small tree and being 2-3 m above the ground. The fourth was a Lycopodium growing over the bank. These four subsites were in linear sequence going up the road and were separated by 3, 2, and 3 m respectively. Other subroosts were located up the road from the main roost, one being a group of dead twigs under a bush 1 m above ground level and 7 m from the main roost and a second consisting of twigs projecting from a liana approximately 8 m above the ground and 70 m up the road. The occupation of these upper subroosts seemed largely a function of disturbance introduced while making observations on arrival times at the main roost.

The times of departure from and arrival on the roosts ranged between 0535 and 0659 hrs and form before 1619 to 1729 hrs, respectively. (Fig. 3). While these behavior patterns are correlated with sunrise (ca. 0600) and sunset (ca. 1800), the precise factors influencing the behavior are not immediately obvious. Light values taken on the morning of March 10 do not provide any additional information in this respect (Fig. 4); however, the individuals at the lower subroost consistently roosted earlier in the evening than those at the main roost, indicating that the increased shade at the lower sites may play some part in the initiation of roosting. Somewhat counter to this are the observations from March 9, when heavy clouds and rain seemed to produce a delay in the initiation of roosting. This was possibly due to the disturbance caused by the rain. Prior to roosting, these butterflies seem very sensitive to movement and may fly from the roost if but slightly disturbed (note Fig. 1).

Of considerable interest is the degree of area faithfulness exhibited by Heliconius erato. Out of a possible 27 returns over four days, 17, and perhaps 19, were realized (Fig. 5). Using the percent of returns as a measure of area faithfulness, it is seen that 63-70 % of the marked individuals returned to the same area over a 2-3 day interval. Moreover, there is no indication that the percent of returns is decreasing with time as would be expected if the butterflies were just moving through the area. These data suggest that individuals of Heliconius erato have well defined home ranges along with the ability to locate a specific area within this home range. The same is possible for H. ~~ethillus~~, a much stronger flier, although the data are too few to be more than suggestive. They serve, however, to elicit questions about the nature of gene flow, inbreeding, and selective pressures exerted by predators and food resources that affect and have affected these localized systems. It was not possible to get reliable data on roost faithfulness due to disturbance introduced while making roosting observations, although some individuals did consistently return to the same roosting site.

As San Vito a comparative study was made on the area and roost fidelity of Dryadula phaetusa over an eight day period. These butterflies were roosting along a southeastwardly facing bank, 2 m high, on a road cut through a coffee plantation. The bank was covered with ferns, grasses, and small dicots approximately 0.5-1 m high. Three roosting sites were intermittently occupied, the first being 7 m up the road from the second, and the second 3 m up from the third. All the sites were between 0.5 and 1 m from ground level. The butterflies variously rosted on the undersides of dicot leaves, ferns, and grass blades, characteristically facing outward from the bank.

Area faithfulness in Dryadula seems very low when compared with Heliconius erato. (Fig. 6). Over the study period only 28 % of the possible returns were observed in the area. Roost faithfulness was much lower, with only 8 % of the individuals returning to the same roost on consecutive evenings.

Of interest is a single nymphaline, Anartia fatima, which roosted at the second site for five of the eight days, in the presence or absence of Dryadula. This Anartia seemed to have a high degree of roost fidelity although the species is apparently not known as a gregariously roosting insect.

Three other species observed roosting at San Vito included Dryas julia, Dione juno, and Heliconius charitonius. Dryas was found roosting on three occasions, in all cases as single individuals under vegetation near 2 m above ground level. Two of the Dione were observed resting together on a roadside annual dicot as was an assemblage of 16 Heliconius charitonius. These roosts were exposed and approximately 0.5 m above the ground.

MORPH FREQUENCIES OF *HELICONIUS DORIS* AT RINCON

The existence of polychromatic populations in distasteful insects is a well known although perplexing phenomenon. Since uniformity in the model population is often considered a necessary selective result of Müllerian mimicry, these discrepancies have usually been accounted for by such phenomena as clinal polymorphism or heterozygote superiority. The alternatives of disruptive selection and multiple co-models are seldom considered.

This study involved a polychromatic population of *Heliconius doris aristomache* near Rincon, Puntarenas Province, Costa Rica. The population sample contained the forms *viridis*, having greenish-yellow rays on the dorsal surface of the hind wings, *eratonius* with red rays, and *luminosus* with light blue rays. Between February 21 and March 11, 1967 a sample of nineteen *H. doris* was taken. Of these, fifteen were of the *viridis* form, three of the *eratonius* form, and one of the *luminosus* form, giving a ratio of 79:16:5, respectively. The form *luminosus* is probably considerably rarer than indicated since no others were seen in a large visual sample. One of the *eratonius* had a basal red patch on the upper forewing. Experimental evidence that these color forms are genetic lly determined has been presented by Sheppard (1963).

The impression obtained from museum material is that *viridis* occurs at "variable but normally low frequency" throughout Surinam to Nicaragua (Emsley 1965). The usual form of the species has a dark blue ray pattern on the dorsal hind wing.

Why should the forms *viridis* and *eratonius* predominate at Rincon? In northwestern Panama and southwestern Costa Rica two other species of *Heliconius* occur that have paired yellow bands on the forewings and a submarginal yellow hind wing bar, giving a superficial *viridis*-type pattern. These two species, *pachinus* and *hewitsoni*, fly in the same habitats as *doris* but are restricted to a small geographic area. During the period of the study nineteen specimens of *pachinus* and *hewitsoni* were collected, although considerably less collecting pressure was directed toward these species than toward *doris*. In fact, these populations were probably in total more than twice as dense as *Heliconius doris*. These factors, along with others to be given below, suggest that selective mimicry could be playing some role.

The *eratonius* form of *doris* seems to correspond to the coloration of an aristolochious swallowtail that exists at relatively low densities in the area. These swallowtails are frequently seen butterflies, but their rapid flight makes them difficult to capture. Selective forces balanced by variable predator experience with the two aposematic color forms is a possible mechanism whereby a stable polymorphism could be maintained. However, clinal polymorphism cannot be excluded. The first hypothesis seems more plausible when one considers that *Heliconius doris* is more acceptible to those birds which have been tested than many other species in the genus (Brower *et al.* 1963,1964b). Thus, the situation could at times of low food availability approach that of a Batesian system. There is no good evidence as to why the dark blue form should be prevalent in some areas, although it might be suggested that this is a case of Müllerian mimicry with *Heliconius sarae*, a species not observed at Rincon but reported from Costa Rica and neighboring countries. Likewise, the alleles causing the dark blue morph might confer a slight physiological advantage which would balance any selective advantage of possessing red or yellow coloration.

With more frequency and morph distribution data plus a firmer knowledge of the genetics controlling this system and comparative viability data under natural growth conditions, it should be possible to elucidate more precisely the selective and non-selective processes regulating polychromatism in *Heliconius doris*.

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