Geographical and ecological expansion in tropical butterflies of the genus Morpho in evolutionary time

by

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ABSTRACT: Selected morphological, behavioral, and ecological traits of Central and South American species of *Morpho* butterflies are examined as an attempt to account for the present day geographical and ecological distributions of the genus in Central America. Emphasis is placed on the successful or unsuccessful adaptive radiations of different species groups at different altitudes, and between primary-growth and secondary-growth plant communities. It is postulated that there were two major successful adaptive radiations of *Morpho* in Central America, characterized today by three species: *M. granadensis* and *M. peleides* into second-growth plant communities in lowland and montane second-growth forests, and *M. amathonte* in lowland primary-growth forests. All three species have extensive geographical ranges where their habitats occur, all are common locally, and at least two of them (*granadensis* and *peleides*) show high sub-speciation and variety. Unsuccessful adaptive radiation, as indicated by the occurrence of small isolated populations and low sub-speciation, is represented in Central American *Morpho* by *M. cypris* in lowland primary-growth forests, and by *M. theseus* in montane primary-growth forests. A possible transitional form between unsuccessful adaptive radiation in montane forests and successful adaptive radiation in both lowland and montane forests is represented by *M. polyphemus.*

"He (Bates) admired the *Morpho menelaus* but said it looked drab in comparison with *Morpho rhetenor,* the wing of which had a luster almost dazzling to the human eye. This form frequented the sunlit alleys of the forests, but flew so high that specimens were almost never captured. It rarely came lower than twenty feet, and when the sunlight reflected from its huge wings it could be seen a quarter mile away. Another closely allied form was *Morpho eugenia.* This species had wings of a satiny-white appearance, and it was just as hard to capture as *rhetenor*".

P. R. Cutright, 1940.
The Great Naturalists Explore South America (MacMillan) p. 317.

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This paper discusses the hypothesis that butterflies belonging to the tropical genus *Morpho* (Lepidoptera; Nymphalidae; Morphinae) are undergoing both successful and unsuccessful evolution (BRIGGS, 1) in Central America. We hypothesize two distinct successful adaptive radiations in Central America, one of these represented today by two species (*peleides* and *granadensis*) of the *achilles* group (SEITZ, 24) and the other by *amathonte* of the *rhetenor* group (series). These adaptive radiations were characterized by two widespread ecological expansions: (a) *peleides* and *granadensis* successfully invading both lowland and montane second-growth plant communities associated with river edges, mud slides, and road clearings; (b) *amathonte* generally restricted to undisturbed lowland primary-growth tropical wet forests. There were also at least two unsuccessful adaptive radiations resulting in very limited and patchy ecological expansions, *theseus* of the *catenarius* series into montane primary-growth forest, and *cypris* of the *rhetenor* group into small isolated patches within lowland primary-growth forests. Finally, one species, *polyphemus* of the *laertes* group represents a transitional species between unsuccessful and successful evolution, where it was formerly associated with lowland primary-growth forests but has successfully invaded second-growth communities at higher elevations. Our criteria for successful evolution in *Morpho* are twofold, high local population densities (productivities), and extensive sub-speciation or development of varieties.

Our support of this hypothesis comes from examining various morphological (wing color, reflectance, surface area), behavioral (adult and larval activities associated with reproduction and/or defense), and ecological (larval host plant specificities, rates of predation and parasitism) traits, determined for some Central and South American species and predicted for others, and to argue how these collectively may account for the different adaptive strategies predicted for the genus specifically in Central America. Emphasis is placed upon adaptive strategies of (a) oviposition, (b) defense behavior of caterpillars, (c) palatability spectra, and (d) strategies of courtship encounters and general flight behavior. Using these and other traits, we account for both widespread (successful) and restricted (unsuccessful) ecological expansions of different groups of species along altitudinal gradients and between primary-growth and secondary-growth habitats at a given altitude. Our model is summarized in Table 1. Recent discussion (JANZEN, 12) of geographical barriers in tropical environments has led us to believe that different species groups of *Morpho* have experienced different selection pressures in lowland and montane tropical forests in Central and South America. Likewise at a given altitude, differences in the stability and complexity between primary-growth and second-growth forest communities result in different kinds of selection pressures for herbivorous species found there.

TABLE 1

Summary of the major adaptive radiations in Central American Morpho *butterflies**

Group	Central American member species	Degree of sub-speciation and variety	Major habitat(s)	Type of evolution	Predicted local adult population densities
Brownish morphos	*peleides;*	high	montane + lowland	successful	high
	granadensis	high	second-growth	successful	high
Dazzling blue morphos	*amathonte;*	low	lowland primary growth forest	successful	low
	cypris	low	lowland primary growth forest	unsuccessful	very low
Chalky white morphos	*theseus*	low	montane primary growth forest	unsuccessful	very low
Glossy White morphos	*polyphemus*	low	montane and intermediate levels of primary and second growth forests	unsuccessful-to-successful (transitional)	intermediate

* Based on observations of *Morpho* in different parts of Costa Rica (1968-1972) and also from a literature survey for all of Central America.

We also emphasize that this report is not an attempt to explain phylogeny within the genus *Morpho;* instead, we wish to point out differences among species groups in terms of present-day ecological and geographical distributions, and to account for these patterns through speculation on evolutionary strategies encompassing observed morphological, behavioral, and ecological traits. And although our emphasis is on the Central American *Morpho,* our findings are applicable to the South American members of the genus as well. In fact, we draw upon various South American species as additional illustrative examples of our views on evolutionary strategies.

GEOGRAPHICAL AND ECOLOGICAL EXPANSION: GENERAL REMARKS

In light of detailed descriptions of wing color patterns both in terms of sexual dimorphisms and geographical variations for many species of South and Central American *Morpho* as presented in SEITZ (24), and from our own studies on the ecology and behavior in a few selected Central American species (YOUNG, 29, 30, 31, 32, 33; YOUNG and MUYSHONDT, 34, 35), we advance the hypothesis that during the early evolution of the genus from a *Brassolis* or *Brassolis*-like ancestral stock (SEITZ, 24; EHRLICH, 8; EHRLICH and RAVEN, 9) which probably occurred in lowland South American tropical wet forest (head-waters of the Amazon), natural selection favored the evolution of various complexes of species that culminated in an ecological as well as geographical expansion of *Morpho* into premontane and montane forests and a variety of second-growth habitats. Concomitantly with these adaptive radiations of *Morpho,* there were major adaptive shifts, including (a) an initial transition in most species to dicotyledonous larval host plants from monocots characteristic of the majority of *Brassolis* and other Morphinae (9), (b) a gradual exploitation of a narrow or restricted range of host plants characterized by toxic secondary substances (probably phenols), (c) a later ecological expansion into second-growth plant communities encompassing a wider range of host plants and comprising a spectrum of toxicity, and accompanied by (d) an invasion into montane tropical wet forests characterized by frequent and low dense cloud cover and their associated cloud-covered passes and ravines. Note that we maintain a transition from monocot to dicot larval host plants for *Morpho.* This is a different view from that of EHRLICH and RAVEN (9) who imply that most butterfly groups diversified on dicots and then secondarily moved on to monocots. But from the standpoint of the phylogeny of the Morphinae, it appears that *Morpho* has evolved from monocot-feeding genera like *Brassolis* (24). And since most species of *Morpho* feed on dicots (9), the general pattern in the transition of larval host plants would have therefore been from monocots to dicots.

Essentially this hypothesis accounts for extensive adaptive radiations (upwards of 30 species and about 140 subspecies) of the genus *Morpho* which are very different from the relatively restricted radiations of the remaining 22 to 25 genera (9) comprising the Morphinae and Brassolinae. For *Morpho,* these radiations have resulted in strong vertical habitat selection in primary-growth, undisturbed forest (in terms of preferred flight activity areas for adults and oviposition sites), and secondarily into disturbed plant communities (second-growth forest; horizontal habitat selection) in the non-seasonal wet tropics (SLOBODKIN, 25). For the remaining genera, there remains a severe restriction to lower regions of heavily-shaded understory in primary-growth forest.

Thus, the ecological expansion of *Morpho* as contrasted with other genera of Morphinae (i.e., *Amathusia, Brassolis, Caligo, Dynastor, Taenaris, Opsiphanes,* and others) entailed a broader exploitation of host plants including a wide spectrum (qualitative and quantitative) of toxic secondary substances. According to our hypothesis, and the limitation of geographical and ecological expansions of butterflies by the distribution of potential larval host plants (DETHIER, 6, 7), a major selective force governing the evolution of *Morpho* has been mimicry and automimicry (32) as mechanisms for escape from predators. Once *Morpho* had begun to exploit upper strata of the forest and exposed second-growth habitats, by virtue of extremely large size, accompanied by the usual low diversity of monocots in such environments (potential larval host plants carried over from *Brassolis),* the genus (both caterpillars and adults) shifted from a protective strategy (predator-defense) of concealment and crypsis that satisfied the relatively minor radiations of other Morphinae (i.e., the majority of these butterflies are dull brown with various shades and lines of yellow or deep blue) on monocots in heavily-shaded forest understory, to a strategy more compatible with the higher predation pressures associated with a greater diversification in habitat. Thus, from ancestral forms which were cryptically-colored and which fed on monocots (i.e., similar to the modern-day *M. hercules* and *M. aega* which are among the darkest-colored of the morphos and whose larvae have been reported to feed on some monocots, COSTA LIMA, 5; EHRLICH and RAVEN, 9) and which were probably highly palatable, there arose a diversification into various species-groups of *Morpho* associated with upper, insolated regions of forest understory, forest canopy, and the open exposed river edges and clearings (resulting from topplings of large canopy trees and localized landslides following heavy rains). As will be discussed in greater depth below, if one examines the types of second-growth habitats exploited by certain species of *Morpho,* such as *peleides* in Costa Rica (34), it is apparent that such species oviposit on a rich variety of legumes that have been characterized by RICHARDS (22) as "pioneer" species associated with recently-formed patches of bare earth along rivers and on mud slides. This tendency for *Morpho* to exploit various types of second-growth habitats was accompanied by geographical expansion into mountainous regions, in which there perhaps occurs a greater incidence of localized forest destruction through the washing away and erosion of soil on slopes following heavy rains. While the actual evolutionary expansion of *Morpho* was certainly much more complex than this, nonetheless, it seems clear that certain groups are more abundant in regions where there have occurred major landslides and destruction of forest, either the result of natural agents of weather, or through the intervention of man. This will be discussed specifically for *Morpho peleides (achilles* group) and *M. polyphemus (laertes* group) in both El Salvador and Costa Rica, where it is apparent that these species have either experienced *(peleides)* or are experiencing *(polyphemus)* strong selection to invade second-growth habitats, often associated with human habitation (34, 35).

"BLUE MORPHOS", "BROWNISH MORPHOS", AND "WHITE MORPHOS"

Ecological expansions in evolutionary time resulted in no less than four major "groups" of *Morpho* butterflies in the present-day fauna. These groups correspond to no phylogenetic scheme of the genus, but rather reflect different strategies of ecological adaptation to tropical environments.

Through correlation of the available fragmentary data concerning the habits of different species (SEITZ, 24; L. OTERO, 20, pers. comms.) and preliminary studies on the ecology of some Central American species (29, 30, 31, 32, 33, 34, 35), coupled with detailed descriptions of wing coloration (24), we propose four groups of *Morpho*, irrespective of phylogenetic affinities: (a) "dazzling blue morphos", (b) "dull-to-glossy brownish-blue (brownish) morphos", (c) "chalky whitish-green and whitish-brown (chalky white) morphos", and (d) "glossy, translucent white (glossy white) morphos". Representative species of these groups are shown in Figure 1. We make these groupings based on phenotypic characters of the wings, especially clarity of coloration, brightness, and reflectance. Great differences in these morphological traits are clearly delineated for most species, thus facilitating the assigment of different species to this arbitrary system of classification. Later, one of us (A.M.Y.) will summarize the patterns of response by human subjects and blue jays to sections of dorsal wing surface of representative species of these groups, when held against various shades of dark green backgrounds (simulating foliage) and under varying types of light, ranging from direct (as in unobstructed sunlight) to very diffuse (as light passing through heavy cloud cover) light. According to this system of classification, the "blue morphos" mentioned in YOUNG (30) refer to dazzling blue morphos here, while the "brownish morphos" in that same publication refer to the dull-to-glossy brownish-blue morphos. Other relevant characters important to the following discussion include the amount of light-colored wing surface area and general shape of the wings — characters which also vary greatly among the four groups (Fig. 1). Furthermore, morphos belonging to chalky white and brownish categories possess the darkest ventral wing surfaces of all four groups. In the case of chalky white morphos, this consists of various shades of deep reddish-brown with reduced ocelli; for the brownish morphos, this color approaches very dark chocolate brown and black, with large ocelli. In dazzling blue morphos, the undersides of wings vary from light reddish-brown (*M. anaxibia* in Brazil) to light tan (*M. amathonte* in Costa Rica) accompanied in most species by very small ocelli. Species of South American and Central American *Morpho* which we have placed into these four groups appear in Table 2. It should be mentioned that *M. polyphemus,* the single species representing glossy white morphos (Table 2), possesses very translucent wings with the ventral surfaces appearing very similar to the dorsal surfaces; the ventral pattern of ocelli is also visible from the dorsal surface (Fig. 1). There occurs a single species of dazzling blue morpho, *M. cypris,* also from Central America, which possesses broad translucent white bands across both sets of wings, exposing dorsally markings of ventral surfaces, including some ocelli. Due to the quantity of white and the nature of its translucent properties in *M. cypris,* perhaps *M. polyphemus* evolved from *cypris* recently, and represents a new adaptive radiation of *Morpho* in Central America. It is difficult to envision glossy white morphos being developed from chalky white morphos since major differences exist between these two groups, to be discussed in detail below.

TABLE 2

Distribution of South and Central American species of Morpho* *among the four groups postulated in Table 1 and representing major ecological expansions in the New World tropics*

Chalky white-brown white-green morphos	Dull-glossy brownish-blue morphos	Dazzling blue morphos	Bright white morphos
hercules (2)	*peleides* (17) C.A.	*aega* (5)	*polyphemus* (2) C.A.
hecuba (7)	*achilles* (12)	*anaxibia* (2)	
perseus (6)	*achillaena* (6)	*lymphairs* (1)	
theseus (10) C.A.	*granadensis* (3) C.A.	*sulkowskyi* (4)	
laertes (2)	*vitrea* (2)	*rhodopteron* (1)	
catenarius (5)	*leontius* (2)	*aurora* (2)	
	patroclus (5)	*adonis* (2)	
	deidamia (6)	*uraneis* (1)	
	rugitaeniatus (1)	*didius* (2)	
		amathonte (4) C.A.	
		rhetenor (4)	
		cypris (3) C.A.	
		portis (4)	
		godarti (4)	
		menelaus (9)	
Taxonomic groups:**			
2	8	4	1
Species:			
6	10	14	1
Subspecies:			
32	59	44	2

* based on a survey given in SEITZ (24).
** the "species groups" given in SEITZ (24).

These four postulated groups of *Morpho* butterflies serve as the basis for discussion of the different strategies of ecological adaptation among different groups of species.

A major finding of this preliminary survey is that each of these postulated groups of *Morpho* represents a different strategy of ecological and/or geographical expansion in evolutionary time. For example, we maintain that the dazzling blue morphos in the modern-day genus exhibit a wide range of specializations, so that member species (Table 2) comprise a kaleidoscope of increased specializations adapted for survivorship and reproduction in primary-growth lowland tropical forests. On the other hand, the brownish morphos (Tables 1, 2), present a different adaptive strategy in which member species (especially *peleides* and *achilles*) are experiencing major ecological expansions into less stable plant communities (second-growth habitats) and along altitudinal gradients into montane forests; these expansions account, in part, for the apparent high subspecies diversification in the group (Table 2). It is the chalky white morphos which retain the most "primitive" ecological and behavioral adaptations of the genus, in which member species are rather restricted to shaded primary-growth forest, and which exhibit ecological and behavioral characteristics usually associated with the Brassolinae or Satyrinae. There has been a restricted geographical expansion of this group into montane forests, as indicated by the modern-day distribution of species (24). We also hypothesize that the single species of glossy white morpho, *M. polyphemus*, represents a very recent development of a lineage from the dazzling blue morphos subsequently moving into second-growth forests at varying altitudes.

ECOLOGICAL PROPERTIES OF THE GROUPS OF *MORPHO*

Table 3 summarizes the major adaptive ecological, behavioral, and morphological traits of *Morpho* according to the four groups outlined above. We caution that most of these predictions, especially regarding dazzling blue morphos, are based on data gathered from only a small number of the species listed in Table 2. Nevertheless, the types of predictions that we are making for all four groups are easily subjected to verification in future field studies. In fact, the apparent clear-cut differences in character states of some of the various traits listed in Table 3 make *Morpho* an exceedingly interesting group to study, since presumably such differences reflect different adaptive strategies and evolutionary histories (MAYR, 18). Since many of the traits listed in Table 3 are either self-explanatory or lacking sufficient data, our discussion is limited to a select group of several traits.

Before discussing these traits, it is necessary to consider briefly the major differences in wing spectral properties among the groups, since it is this morphological character which forms the basis for much of our predictions on adaptive strategies. From earlier measurements of reflectance properties of dorsal wing surfaces from various species (30), brownish morphos possess relatively low reflectance in direct sunlight, as compared to the dazzling blue morphos, whose reflectance properties can approach those of perfect mirrors. In direct sunlight, dazzling blue morphos are a great deal more conspicuous than the brownish, even though both types possess similar wing movements, characterized by strong flapping motions. However, the flight pattern of at least one species of dazzling blue morpho, namely *M. amathonte* is further characterized by strong bobbing motions while that of brownish morphos *(peleides, granadensis, achilles, achillaena)* tends toward being more even. In contrast, the wing reflectance properties of chalky white morphos are virtually zero, and those of the glossy white morphos, *M. polyphemus,* are similar. Thus in direct sunlight, to the vertebrate eye, dazzling blue morphos appear the brightest, followed in descending order by brownish, chalky white, and glossy white morphos. A very different pattern emerges when these butterflies are viewed in diffuse light, simulating light passing through heavy cloud cover. Here, for reasons of contrast, the glossy white morphos are now the "brightest", followed by brownish and chalky white morphos tied in rank, with dazzling blue morphos being the least conspicuous. This effect is appreciated to some degree by a glance at the butterflies in Figure 1.

It has been pointed out (ROTH and BIFANO, 23) that tropical cloud forests, defined here as montane forests within 700 to 1300 meters elevation, are characterized by heavy cloud cover just above the canopy for most of the day. Under such persistent conditions, there may be strong selection in certain organisms to adapt phenotypically to the presence of cloud cover, if some advantage were gained through selection. In the case of chalky white and glossy white morphos, whose ranges are predominantly within the montane forest range of 600 to 1100 meters (20, 24), a selective response could be envisioned for the evolution of white or whitish wings, since under conditions of diffuse light, white is very conspicuous against various shades of green (simulating foliage backgrounds). Along the same line of reasoning, the prediction is made that predominantly blue morphos will be restricted to lowland wet and premontane forests where there usually occurs great incidence of direct sunlight striking the canopy through most of the day (22), thus setting up ideal conditions for dazzling blue morphos to be especially conspicuous against the foliage backround. Underlying these predictions is the necessity for these butterflies to be unacceptable as prey, since selection seems to favor increasing conspicuousness against foliage while the insects are flying.

DAZZLING BLUE MORPHOS: We maintain that this group represents a primitive cluster of morphos that probably evolved from a stock of *Brassolis,* and which gave rise to glossy white morphos. The dazzling blue morphos represent the successful adaptive radiation of the genus in the lowland wet forests of Central America. Close evolutionary affinity with *Brassolis* is suggested by the marked sexual dimorphism (Table 3) characteristic of virtually all species under this category (Table 2). Here, the females are generally ochreous to brown, although in some species, the brilliant blue of males reappears in the form of reduced regions of the proximal wing surface. Only the males, however, appear to possess the highly reflective properties discussed above. While there exists some geograpic variation in most species (24) this is not as extensive as seen in members of the brownish morphos; dazzling blue morphos, while existing in an array of subspecies associated with different regions of primarily

TABLE 3

Selected adaptive traits predicted for the majority of species of Morpho *belonging to four distinct groups, postulated primarily on the basis of wing coloration, brightness, and reflectance (see text)*

Traits	Chalky white-brown white-green morphos	Dull, glossy brownish-blue morphos	Dazzling blue morphos	Glossy white morphos
General				
Genetic variability	low	high	low	moderate
Geographical distribution	narrow	wide	narrow	wide
Number of subspecies; varieties	low	high	moderate	low
Major local habitats	primary-growth montane forest	second-growth lowland + montane forests	primary-growth lowland forest	montane primary-growth
Productivity	low	high	low	moderate
Major altitude preference	montane (500-1000 m)	lowland and montane (28-1000 m)	lowland (28-100 m)	montane (500-1000 m)
Adults				
Range of lightest color(s) on dorsal wing surface	great	small	great	great
Brightness of wings	low	low	high	high
Reflectance of wings	low	moderate	high	low
Geographic variation in wing color	narrow	wide	narrow	narrow
Sexual dimorphism in wing color	weak	weak	strong	weak
Major habitat for flying	between canopy and lowest cloud cover	low over exposed second-growth	canopy and sunlit areas of understory	canopy and second-growth
Diurnal feeding pattern	midday or crespuscular	late morning, PM and crespuscular	morning	all day

Major food sources	leachates and fungi	fungi and fruit	fruit and fungi	fruit
Diurnal flying pattern	late morning, afternoon	late morning, afternoon	morning	all day
Flying pattern	soaring and gliding	rapid flapping	rapid flapping, and bobbing	soaring
Rates of predation	moderate	moderate	low	low
Acceptability as prey	moderate	moderate to high	low	low
Type of oviposition	cluster	single	triplet, doublet, single	single
Major oviposition site	emergent canopy	low second-growth	canopy, possibly forest clearings	canopy* or low second-growth
Eggs, larvae				
Rate of egg parasitism	low	high	moderate	high
Local host plant specialization	narrow	wide	moderate	narrow to moderate
Acceptability spectrum of larvae to predators	narrow	wide	moderate	narrow to moderate
Major skew of acceptability spectrum	acceptable	intermediate	unacceptable	unacceptable
Diurnal feeding pattern	nocturnal	dawn-dusk	nocturnal	dawn-dusk
Gregarious/non-gregarious resting behavior	gregarious	non-gregarious*	gregarious to non-gregarious	non-gregarious
Rate of larval parasitism	low	high	moderate	high
Rate of predation on larvae	low	low	low	low
Developmental time	long	short	long	intermediate
Life table (Survivorship curve)	near-diagonal	diagonal	rectangular	near-rectangular
Species diversity, local	low	low	high	low
Monocot (M)/Dicot (D) host plants	D	D	M, D	D
Local dicot exploitation at:				
(a) Family level	low	low	high	intermediate
(b) Generic level	low	high	low	high

South America with only minor representation in Central America *(amathonte* and *cypris)*, tend to be restricted to lowland tropical wet and premontane forests, rarely occurring above 400 m elevation. The majority of species are active at the sunniest hours of the day (24, 29) and make very conspicuous flight patterns above the forest canopy and through clearings and along streams; the bulk of adult activity is restricted to habitats where there is maximum exposure to sunlight. Most species have regular flight paths through or over the forest, consisting of male home ranges and perhaps even territories in some species (33). Males are strikingly more mobile than females which remain fairly concealed in forest understory or under the canopy vegetation. The rather cryptically-colored females adopt a courtship strategy in which they position themselves along flight paths of males, interacting visually with them over short distances as a prelude to copulation.

Local adult population densities are the lowest for all four groups, the result of selection for both low physiological and ecological fitness (ISTOCK, 11) rendering them to be well-integrated into the primary-growth tropical wet forest community. While the evolution of predictable flying behavior in males permitted a courtship strategy in which cryptically-colored females remained concealed most of the time in low adult density populations, such conspicuous activity of males was made possible through the development of effective defense against predators. Therefore, in most member species of this group, we predict, relative to brownish morphos and chalky white morphos, restriction of larval feeding to a narrow range of host plants, the majority of which render the insects unacceptable as prey. It has been demonstrated that various butterflies are unacceptable to avian predators (BROWER, BROWER, and CORVINO, 3) and that this property results from ingestion of plant tissue containing toxic secondary compounds (LEVIN, 14). From their apparent close affinity with the Brassolinae, we predict that some species may be partially unacceptable as prey, feeding on a spectrum of host plants that includes some which are not high in toxic secondary compounds so that there may exist small complexes of automimicry (BROWER, 2) in which most individuals are in fact unacceptable. However, relative to brownish and chalky white morphos, this system of automimicry is neither characteristic for all species in the group, nor does it involve as broad a spectrum of larval host plants as predicted for any single species of brownish or chalky white morpho. Thus while dazzling blue morphos may be highly unacceptable as prey, this is a very variable character among different species, according to the degree of automimicry involved. Although never attaining the broad spectrum of local acceptable and unacceptable varieties that we predict for other groups, these butterflies have evolved pursuit stimuli for inviting predator attack and foiling it (30) in addition to being partially toxic as a local population. Both of these defenses against predators (reduced automimicry and predator foolhardiness) result in high local survival of adults unparalleled in other groups of *Morpho* (31,32) and rates of predation upon adults is very low. While most species belonging to *Brassolis* possess gregarious larvae which feed on a variety of monocots (24), we predict that the majority of species of dazzling blue morphos feed on Sapindaceae and to a lesser extent on Leguminosae, with larvae retaining the Brassolid trait of gregariousness. *Morpho aega,* which in both sexes comes to resemble *Brassolis* very closely, has been recorded from bamboos (Gramineae; EHRLICH and RAVEN, 9) and may well represent the ancestral-type for the dazzling blue morphos.

The prediction is also made that oviposition in most species of dazzling blue morphos will range from cluster oviposition, to single oviposition in which more highly evolved members of the group lay fewer eggs singly or in very small groups close together on the same leaf or adjacent leaves. Cluster oviposition, carried over from *Brassolis,* results in the reproductive effort of the local population being concentrated over a relatively small area of the habitat and highly dependent upon the positions of concealed or hiding females which remain relatively immobile (LABINE, 13). For the majority of highly evolved member species (Table 2), oviposition sites will be concentrated in the upper strata of lowland forest, especially on Leguminosae and Sapindaceae, emergent in the canopy.

However, there exists an apparent evolutionary trend within this group for feeding on dicots. L. R. Otero (pers. comm.) has recently reported that *Morpho aega, M. portis, M. adonis,* and *M. sulkowskyi,* which are all members of this group in our classification (Table 2), feed on Gramineae. This places these species very close to the Brassolids or Satyrinae and makes them primitive dazzling blue morphos. In these species, as in the most "Brassolid-like" species of chalky white morphos, namely *M. hecuba* and *M. hercules,* there is very strong egg clustering on host plants, and larvae form large aggregations which persist through all instars, but disperse as prepupae. It is generally mentioned that many Brassolids lay eggs in clusters (24), and more recently confirmative documentation of this has been obtained for certain species in El Salvador: *Caligo memmon* and *Tisiphone maculata,* with the former on *Heliconia platistachus* and *Musa paradisiaca,* and the latter on various species of bamboos. Cluster oviposition in *Caligo uranus* on various Palmae in heavily-shaded forest understory in lowland tropical wet forest in the Caribbean lowlands of Costa Rica has also been observed. However, it is clear that not all Brassolids have cluster oviposition, suggesting once again that different Brassolid lineages may have given rise to different lineages of *Morpho: Opsiphanes tamarindi* always lays eggs singly on many kinds of Musaceae, and *O. cassina* oviposits singly on many species of Palmae. Dazzling blue morphos may have arisen as a lineage from a Brassolid stock characterized by cluster oviposition as seen in certain modern-day genera like *Caligo,* while other groups of *Morpho,* such as the brownish morphos in which oviposition is always single and larvae are never gregarious, could have arisen from a different Brassolid stock in which single oviposition as exemplified in genera such as *Opsiphanes* was the rule. We also know that within the dazzling blue morphos there occur other species in which oviposition is single, double, or in triplets. Such oviposition appears to be correlated with the more showy species of this group, such as *Morpho anaxibia* (L. R. Otero, pers, comm.) which may suggest an adaptive radiation of *Morpho* into the canopy of tropical forests.

That is to say, accompanying an ecological expansion of dazzling blue morphos vertically in tropical forests, with respect to habitat selection for optimal foraging and breeding spaces, there evolved a breakdown in cluster oviposition favoring a greater dispersion of reproductive effort, higher than that characteristic of most genera of Brassolids. However, relative to the brownish morphos and the glossy white morphos (Table 2), this dispersion of reproductive effort was small. Within the group, we see a wide array of wing brightness in males, and we predict a correspondingly broad spectrum in cluster oviposition. For example, *M. menelaus* is not as bright as *M. rhetenor*, thus we predict that clustering is more probable in *menelaus*. It is also possible that with the exception of a small cluster of South American species (*Morpho aega, adonis, portis,* and *sulkowskyi*), virtually all other species of dazzling blue morphos have lost cluster oviposition, or have reduced it to oviposition in pairs or triplets. We cannot determine the precise transition point in the modern fauna without further detailed study of oviposition patterns in most species of this group (Table 1). It would be interesting to know if single oviposition in this group evolved in response to the transition in larval feeding from monocots to dicots. We know that the understory flora of lowland tropical forests contains large populations of Palmae (22) but of few species. In contrast the dicots associated with the same habitats are extremely diverse. Therefore, it is conceivable that one prerequisite for the successful exploitation of dicots as host plants by *Morpho* would be the ability for ovipositing females to search and discover sufficient numbers of particular dicot species (i.e., various Leguminosae, etc.) whose populations are less dense than monocots under spatial arrangements of host plants. The reduction of mean cluster size and the evolution of single oviposition would be strongly favored by natural selection, in response to the very high diversity of dicots in these forests (PIRES, DOBZHANSKY, and BLACK, 21).

It is of interest to point out that darker species of this group which do not feed on monocots, generally feed on various Leguminosae, while lighter species (the most dazzling blue morphos such as *rhetenor, amathonte,* and *cypris*) apparently feed mainly upon other groups, notably Sapindaceae as does *M. polyphemus.* Most species of brownish morphos, another generally dark group, also feed mostly on Leguminosae, although one sub-species of *M. peleides*, namely *insularis*, has been recorded from *Paragonia pyramidata* in the Bignoniaceae (Malcolm Barcant, pers. comm.). In this connection, it is interesting to note that in the current system of classification (from Bessey's to the more recent ones) the Leguminosae are relatively closer to the primitive Ranalean group than either Bignoniaceae or Sapindaceae. And due to the fact the Leguminosae is a very large and diverse plant group containing about 400 genera (STEBBINS, 27), it may very well have provided the ideal "stepping stone" for the radiation of *Morpho* into new adaptive zones in which dicots became the major larval host plants.

Egg parasitism by various hymenopterans will be very high, although mortatility of the gregarious larvae from predators and parasites will be low, with the major single exception of parasitism by tachinid flies which lay their eggs directly on plant tissue rather than on larval integument. Gregarious behavior in the larvae of the dazzling blue morphos is presumably accompanied by effective collective defense movements and in some species, enclosure within silken webs. Such mechanisms discourage active attack by ovipositing parasite and leaf-roaming predators such as ants, jumping spiders, and predatory hemipterans, but are totally ineffective against tachinid eggs which can be ingested during usual feeding. Unlike the Brassolinae, the gregarious larvae of these morphos have developed extremely gaudy coloration to advertise their presence, presumably as a result of the exploitation of toxic host plants. Nevertheless, due to reduced systems of automimicry existing in lieu of total unacceptability in some species (which is a function of the pattern of local host plant exploitation), larvae have become nocturnal or dawn-dusk feeders (SEITZ, 24; YOUNG, 32, respectively) as further insurance against biotic mortality factors. Relative to brownish morphos and chalky white morphos, we also predict that dazzling blue morphos have the longest developmental times of all groups, as a consequence of long term selection for integration of such species into stable tropical communities (MARGALEF, 17). It is this group that dominates the truly non-seasonal lowland wet tropics in South and Central America (25); other groups have undergone major adaptive radiations in other kinds of tropical environments and in response to different sorts of selective pressures resulting in markedly different states of adaptive traits (Table 3). We must point out that within a large group such as the dazzling blue morphos, there are obviously great variations in the characters discussed above, but that a general pattern is seen for the entire group. If one had to envision an "evolutionary trend" in this group, it would involve, as in the other groups of *Morpho,* a gradual loss in gregarious larval behavior and cluster oviposition, as well as a loss of the marked adult sexual dimorphism in wing coloration in response to a more efficient courtship strategy. From the discussion to follow concerning brownish and chalky white morphos, it is clear that these two groups exhibit the greatest departures from the ecological and behavioral statistics predicted for dazzling blue morphos, in response to ecological and geographical expansions unparalleled in the latter group.

The above considerations are not meant to imply that no representative species of dazzling blue morphos are found outside non-seasonal habitats. In the vicinity of Rio de Janeiro, Brazil, *Morpho anaxibia* and *M. portis* (Table 2) show peak adult populations during the dry season, as do several other species *(laertes, hercules, menelaus, achillaena)* of different groups, but in the Amazon Basin all of these species are abundant throughout most of the year (L. R. OTERO, pers. comm.). Such habitat differences in seasonal abundance patterns in *Morpho* are most likely the result of physiological water stress on larval host plants (35).

GLOSSY WHITE MORPHOS: The single species of glossy white morpho, *Morpho polyphemus* from Central America, represents a very recent evolutionary lineage being developed from a stock of dazzling blue morpho, probably from *M. cypris.* Whether or not *polyphemus* evolved from *cypris* cannot be determined at the present, although it might have been derived from a lineage giving rise to *cypris*. Although SEITZ (24) places *polyphemus* within a different species group than that containing *cypris*, the similarity of ocelli pattern, translucent condition of the wings, and the development of pure white coloration in both species suggest relationship. Like *polyphemus*, *cypris* is also very lightly colored on the ventral surfaces of the wings, one of the lightest of all the dazzling blue morphos. Our thesis regarding this group is that it primitively extended the range of the dazzling blue morphos into high altitudes but has secondarily reinvaded lowland habitats, especially those heavily disturbed by man (35).

Larvae of *Morpho polyphemus* feed on *Paullinia pinnata* (Sapindaceae) near San Salvador (600-950 m), and to a lesser extent, on various legumes such as *Inga* spp. and *Machaerium salvadorensis*. The major larval host plant, however, is *Paullinia pinnata*, which has been reputed extremely poisonous to fish (35), and presumably makes *M. polyphemus* very unacceptable to vertebrate predators. From our studies in El Salvador (35) we maintain that this species possesses a narrow range of larval host plants similar in breadth to those possessed by most species of dazzling blue morphos, but different in the sense of a different strategy of habitat exploitation seen in *polyphemus*. We maintain that *polyphemus* represents the geographical expansion of the dazzling blue morpho lineage into montane (cloud forest) forests of Central America in which selection favored the development of very white wings as a mechanism of contrast, rather than reflectance as in the dazzling blue morphos of the well insolated lowlands, to render the flying butterflies conspicuous against the foliage background. As outlined earlier, this mechanism of brightness is more effective in diffused light environments such as cloud forests than would be a system of high reflectance in which light blue coloration in direct sunlight can also account for high brightness in lowland wet forests. Because the strategy of conspicuousness employs the effect of contrast of white against green, there would be selection for a flight pattern allowing maximum exposure of wing surface to light per unit time, and this appears as a soaring flight movement in *M. polyphemus*. Unlike the undulating and rapid wing motions of dazzling blue morphos, *M. polyphemus* has a strong wing movement involving substantial periods of soaring, allowing prolonged exposure of the white surfaces to the sunlight, diffused through cloud cover.

Associated with the almost total lack of sexual dimorphism in wing coloration (Table 2), we predict a strategy of courtship in which both partners actively seek out one another through extensive flying activity. Both sexes, unlike dazzling blue morphos, should have completely overlapping daily peak flying periods. Eggs are laid singly and scattered over many individual host plants, and mortality of eggs, like in dazzling blue morphos, is high, due primarily to hymenopterous parasites (35). Caterpillars are not gregarious on host plants, although several may occur on an individual plant; larval mortality is high, due to tachinid parasitism and never hymenopterous parasitism (35). It is very unlikely that caterpillars are successfully attacked by predatory insects or spiders, and even vertebrates, due to the presence of a defense secretion giving a very strong vinegar-like odor which is evoked upon physical contact.

If the glossy white morpho form evolved from dazzling blue morphos, we must account for the apparent loss of cluster oviposition and gregarious larvae during this transition. Along this line, it would be very helpful to explore the biology of *M. cypris* (at present undetermined) since we predict close affinity of this species with *polyphemus,* and it may represent a transitional form. We account for single oviposition and non-gregarious behavior of larvae in terms of selection towards greater population dispersion and also in terms of the types of habitats where this species is found.

On this latter point, like the brownish morphos to be discussed below, *Morpho polyphemus* may be thought of as a colonizing fugitive species, one capable of invading and exploiting the second-growth plant communities associated with higher altitudes in tropical regions of Central America. During its early evolution it was undoubtedly a species that depended upon primary-growth wet forest for breeding, as it still does on the Osa Peninsula in Costa Rica (35). However, it later developed into a species capable of successfully carrying on breeding activities in highly disturbed second-growth habitats. While retaining its high unacceptability through larval host plant selection, it evolved automimicry allowing it to "cross physiological barriers into new adaptive zones" (EHRLICH and RAVEN, 9; our quotation marks) encompassing new host plants, some of which rendered individuals acceptable as prey. At least one genus of Sapindaceae was continued to be exploited in second-growth habitats, namely *Paullinia.* It is very likely that adults completing their life cycle on *Paullinia* represent the least acceptable prey of a local population. This however, awaits experimental verification in the laboratory. The ability of this species to feed on second-growth legumes (35) attests to the evolution of a broader host plant spectrum and possibly automimicry. Selection would be especially favored for the loss of cluster oviposition in a colonizing species since it is beneficial to spread reproductive effort out over larger portions of the habitat, rather tham in non-colonizing episodes (LABINE, 13). From recent discussion of the genetic and ecological traits predicted for colonizing species (LEWONTIN, 16), a higher reproductive rate is predicted for *M. polyphemus* as compared with species of dazzling blue morphos. Since most known species of tachinid parasites which oviposit on plant tissue rather than directly upon the host usually disperse eggs over large areas of the habitat on specific plant species (SIMMONDS, 26), the oviposition strategy of *polyphemus,* in which eggs are also dispersed over a large area of the habitat, would result in higher levels of tachinid parasitism than predicted for dazzling blue morphos, where oviposition is clustered and extremely localized for fecundated individual females.

In Costa Rica, *M. polyphemus* is primarily found in the southwestern region of the country (35) where it frequents premontane tropical wet forest (300-400 m elev.). In El Salvador, where virtually all virgin primary-growth forest has been cleared away, the species is abundant in the heavily-disturbed second-growth plant communities associated with streams and often amongst small villages. This close co-habitation of *M. polyphemus*, or any other species or *Morpho* for that matter, with man is never seen in Costa Rica, with the single exception of the subspecies *hydorina* or *M. peleides* (a brownish morpho) which commonly visits refuse dumps of cheese factories at Monteverde in the montane wet forest (1000 m elev.) in the Province of Alajuela. Even here, however, breeding populations do not thrive within the village but rather adults forage there. Thus it appears that *M. polyphemus* has been able to exploit heavily disturbed habitats associated with man, offering further credence to it being a colonizing species. No species of dazzling blue morpho has been noted to possess this capacity in either South or Central America.

In Costa Rica, *M. polyphemus* is primarily a canopy dweller and as such, does most of its feeding in the adult stage off the ground. While brownish morphos, chalky white morphos, and to a lesser extent, dazzling blue morphos feed on decaying fermenting fruits on the forest floor (20, 24, 29, 31, 32), the glossy white morpho seldom forages near or on the ground. From studies of adult feeding activity in *M. peleides* (brownish morpho) and *M. theseus* (chalky white morpho) at Cuesta Angel de Sarapiqui in Costa Rica, we predict that Costa Rican *M. polyphemus* feeds on arboreal odorous food sources, primarily mold patches on tree bark, decaying but hanging fruits of *Philodendron* spp., (Araceae) and the leachates associated with dense epiphytic growth near the canopy. It has been pointed out (MYERS, 19) that dense epiphytic growth is a major physiognomic trait of montane tropical wet forest or cloud forest. This high density, plus high turnover in living plant tissue of epiphytes and heavy rainfall, would favor the continual presence of dripping leachtes from festooning growths of these plants in canopy trees. One of us (A.M.Y.) has observed *M. peleides* and *M. theseus* feeding on very moist decaying epiphyte growth at Cuesta Angel (June-August, 1971). Since adult *M. polyphemus* feeds arboreally, there has been selection for maximum exposure of the undersides of wings while feeding is going on — would-be predators are aware of the presence of these butterflies, the majority of which in a local adult population would be completely unacceptable, and thus avoid them. A simular argument could be made for the partial closure of wings during oviposition on exposed vegetation in the canopy or low second-growth. We do not yet know the complete array of typical adult food sources in the heavily-disturbed second-growth habitats of this species in El Salvador (San Salvador region), although decaying human feces may turn out to be a major food source. One of us (A.M.) has, however, witnessed adult feeding in *M. polyphemus* in San Salvador, where the butterflies, like *M. peleides* there, feed at the fallen fruits of mango, guayava, and jocote (*Spondias* sp., Anacardiaceae). It is interesting to note that *M. peleides* at Cerro Verde (montane forest) in El Salvador feeds at molds associated with arboreal regions of large trees (YOUNG and MUYSHONDT, 34). In connection with the marked conspicuousness of adult *M. polyphemus* during feeding, it is interesting to note that it is the translucent condition of the wings (Fig. 1) that enhances the contrast against foliage; thus there has been selection for maximal contrast properties of white wings in this buteterfly, enhancing predator-recognition and mate recognition during courtship encounters, which are assumed to occur over large distances in the air (in contrast to dazzling blue morphos where females must be relatively close to males for courtship to begin).

Of all four groups postulated here, the glossy white morpho represents a recent divergence in adaptive strategy for species belonging to the dazzling blue morphos, and this has only happened in Central America. And while we cannot account for the precise factors leading to such a divergence, they probably involved positive selection pressures for the evolution of a montane or cloud forest species which is very unacceptable as prey and which employs a strategy of color contrast (as opposed to color reflectance) to advertise presence to potential predators under conditions of continual diffused light. While automimicry may be occurring, this is predicted to be more prevalent in geographical areas where *polyphemus* has become a colonizing species in heavily-disturbed second-growth habitats (i.e., El Salvador as opposed to Costa Rica), in which automimicry is an adaptive strategy, permitting greater exploitation of various larval host plants setting up a spectrum of unacceptability ranging from completely unacceptable (i.e., *Paullinia* feeders) through very acceptable (feeding on certain legumes). Further positive selection pressure for the occurrence of unacceptable glossy white morphos in montane tropical forest would be their possible role as Batesian or Müllerian models for chalky white morphos, to be discussed.

DULL-GLOSSY BROWNISH-BLUE MORPHOS: It is this group of *Morpho* butterflies which has undergone the most extensive and successful geographical and ecological expansión both in South and Central America; this is partly indicated by the high number of subspecies seen for the group as a whole (Table 2), although the majority of these may be attributed to a few South American *(M. achilles, M. achillaena)* and Central American *(M. peleides, M. granadensis)* species.

Morpho achilles in South America and *M. peleides* in Central America represent two major adaptive radiations of the brownish morphos, and SEITZ (24) goes as far as to say that *peleides* is the northern extension of *achilles*. The brownish morphos apparently arose from a separate stock that evolved from *Brassolis*, perhaps independently of the evolution of the dazzling blue morphos. We hypothesize that while they certainly evolved within lowland tropical wet forests, their major geographical and ecological expansions have taken them into montane tropical forests, and perhaps more significantly, into second-growth habitats in lowlands and mountains. In Central America, it is species such as *M. peleides* and *M. granadensis* that are most commonly identified with various successional stages of second-growth wet forests, and their abundances locally far excell the abundance of *M. polyphemus*.

These butterflies represent an ancient expansion into second-growth plant communities, where their distribution is determined by the availability of suitable larval host plants, these being primarily members of the Leguminosae. While virtually all species of the group are predicted to occur in second-growth habitats within primary-growth forests (i.e., along streams, localized clearings, etc.), local adult populations will be highest in extensive second-growth habitats such as those associated with land clearings that have been allowed to grow back. It is this group of *Morpho* that contains species capable of colonizing second-growth plant communities, much more so than *M. polyphemus*, a species of glossy white morpho which represents a relatively recent expansion of the very unacceptable blue morphos into montane wet forests. In contrast to both dazzling blue and glossy white morphos, the brownish morphos are characterized by high rates of predation by birds, reptiles, and perhaps amphibians upon flying and resting adults. Also, unlike the dazzling blue and glossy white morphos, species of brownish morphos such as *M. peleides* and *M. achillaena* are characterized by a broad spectrum of larval host plant specificities (20, 32, 35) leading to the evolution of large complexes of automimicry in which there occur varying proportions of acceptable and unacceptable varieties of individuals in local populations. For example, *M. achillaena* has been recorded from several genera of Leguminosae in Brazil, most notably *Machaerium, Dalbergia, Pterocarpus, Myrocarpus,* and *Platymiscium* (20); in Costa Rica, *M. peleides* successfully completes its life cycle in the field on several legumes, including *Mucuna urens, Machaerium seemanii, Machaerium donnell-smithii,* two species of *Inga,* and at least one species of *Pithecolobium,* with oviposition occurring on all of these plants within a single locality (32, 35). We believe that such local broad host plant acceptance in *M. peleides* and other species of brownish morphos endows a system of automimicry in which potential predators encounter large numbers of both acceptable and unacceptable individuals as they forage through a local adult population, thereby inflicting substantial mortality. However, owing to selection for high intrinsic rates of natural increase (16), such predation is counteracted by high recruitment. Local adult populations of *M. peleides* in Costa Rica appear much denser than for dazzling blue morphos such as *M. amathonte* and *M. cypris* from data obtained on population densities of these species at fermenting fruit baits and from general observations on flying individuals in different kinds of vegetation. Mark-resight studies of *M. peleides* indicate that day-to-day movements of individual males is extremely erratic, although movement appears confined to the same general vicinity of the habitat; such results suggest that at least one species of brownish morpho is characterized by irregular flight behavior, in which large tracts of forest (as contrasted with dazzling blue morphos) are traversed by individuals each day, and that these vary greatly from day-to-day. Such behavior fits in well the general conception of these species as pioneer forms of second-growth; similar data further suggest that females are even more irregular in flying strategy, presumably in response to the need to locate suitable host plants for oviposition. Observations on members of the *achilles* group in Brazil suggest that these brownish morphos have similar flight habits (24).

Like *Morpho polyphemus,* oviposition in brownish morphos is single, so that reproductive effort is spread out over large areas of the habitat; caterpillars are probably never gregarious, and rates of parasitism on eggs by hymenopterans is high. Rates of tachinid parasitism are predicted to be very high on caterpillars, although parasitic attack by hymenopterans will be very low. As in larval *M.*

polyphemus, caterpillars of *M. peleides* are capable of emitting a strong vinegar-like odor upon mechanical stimulation (34). We have observed this for larvae reared on *Mucuna* and *Machaerium*, although relative strengths of secretions by caterpillars raised on these and other host plants are not yet available. As with *M. polyphemus*, we predict an array of qualitative and/or quantitative differences in the chemical secretion corresponding to the spectrum of secondary compounds established by local patterns of host plant exploitation and automimicry, although this range will be much broader for brownish morphos such as *M. peleides* and *M. achillaena*. The dull-to-glossy reflectance properties of species in this group is the result of compromise between selective forces favoring development of unacceptable forms and selection favoring broad host plant exploitation associated with colonizing of second-growth habitats. Superimposed upon this are altitudinal effects in which darker subspecies are more prevalent at higher altitudes, permitting partial crypsis in diffuse light. This darkening is the result of two features: broadening of the marginal brown or black band, and darkening of the basal portion of the blue area of wings. There persists in virtually all species of this group a very dark ventral surface in the wings, including line patterns and large ocelli; these characters aid in camouflaging the butterflies when feeding on the forest floor, and thus contribute to the overall partial crypsis of most species. Predation on feeding adults of *M. peleides* does presumably take place, since specimens have been collected with perfectly symmetrical rounded sections of both hindwings missing, suggesting rear-approach attack by small reptiles or amphibians (34).

Caterpillars of one subspecies of brownish morpho, *M. peleides limpida*, have been studied carefully with respect to their diurnal feeding patterns. The brightly colored larvae, which occur singly on host plants, have a very well defined dawn-dusk feeding behavior, whose function has been interpreted as reducing the risk of predation, even though partial protection is afforded through automimicry in local populations (32). Although other species of brownish morphos have not been studied in this way, it is known that caterpillars of *M. peleides insularis* feeding on *Paragonia pyramidata* (Rich) (Bignoniaceae) in Trinidad usually feed between 7:00 and 9:00 PM (Malcolm Barcant, pers. comm.). Dawn-dusk larval feeding may be prevalent in many species of brownish morphos as an additive mechanism for lowering rates of predation where complex protective systems of automimicry offer partial protection. Presumably, however, such protection would not apply to arthropodan predators, since one species of wasp, *Polistes canadensis* ("Jack Spaniard") on Trinidad attacks and kills large numbers of first and second-instar larvae of *M. peleides insularis* in the laboratory (Malcolm Barcant, pers. comm.), but rates of predation on the larvae in natural populations by this wasp are not known.

Being species most characteristic of various types of second-growth plant communities, most species of brownish morphos will have developmental times shorter than those of the majority of dazzling blue morphos, or even the glossy white morpho, *M. polyphemus* (since this species represents a more recent evolutionary divergence and selection pressures have not yet fully adjusted this ecological statistic to invasion of second-growth plant communities). A short developmental time is another essential attribute of colonizing species (COLE, 4; LEWONTIN, 16). Several persons, working independently in different parts of the New World tropics (Barcant in Trinidad, Muyshondt in El Salvador. Otero in Brazil and Young in Costa Rica) have found similar developmental times for three subspecies of *M. peleides (hyacinthus, insularis,* and *limpida)* and *M. achillaena* (20), all of these being about 3 months from egg to adult eclosion. The developmental time of *M. polyphemus* is, however, significantly longer (35).

In summary, the brownish morphos are most characteristic of tropical second-growth plant communities over a range of altitudes, and also replace dazzling blue morphos in primary-growth forests at high (400-1000 m) altitudes. They show the greatest amount of adaptive radiation, and maybe, in a sense, of tracking the environment (LEVINS, 15) as new second-growth habitats become available throughout the tropics. They possess an array of life history and other ecological statistics which permit most of them to be successful colonizing species while at the same time inhabiting more stable plant communities such as virgin forest.

CHALKY WHITISH-GREEN, WHITISH-BROWN MORPHOS: This group probably represents an independent divergence of the genus from *Brassolis* in which a great many features of this group have been retained, especially with respect to the very clear-cut gregarious habit in terms of both oviposition and larval behavior. This divergence occurred as a selective response to adaptive radiation into primary-growth montane forests and cloud forests. The large array of morphological and behavioral characters of this group (Table 3) suggests that this adaptive radiation was independent of that of the brownish morphos into high altitude forests, as well as that of the glossy white morpho lineage. It is apparent that many species belonging to this group (e.g, *M. catenarius, M. laertes)* are found at higher elevations, usually between 500-1000 meters, and sometimes occur at even higher elevations in the Andes (24). But adaptive radiaton in Central America has been limited to a single species, *M. theseus,* and very few subspecies occur.

It is predicted that few of these species would exhibit the ecological properties of brownish morphos as related to their role as pioneer species, with most species being restricted to primary-growth virgin forest. Observations on *M. theseus* in Costa Rica suggest very limited and patchy (geographically) distributions to montane wet forests and their ravines and passes, with most adult activity confined to the forest canopy. Unlike brownish morphos such as *M. peleides,* which have extensive local adult populations, those of chalky white morphos such as *M. theseus* are very small and localized, each consisting of a few individuals, as indicated by marking studies at transects of fermenting fruit baits in montane forest of Costa Rica. The flying movements of adult males and females, which fly at the same times of the day, are characterized by slow and short periods of gliding interspersed with even shorter periods of actual wing flapping; there often occur extended periods of almost motionless hovering.

Like *M. polyphemus,* this species possesses a flight pattern that permits a maximum exposure of the dorsal surfaces to diffuse light. Movements are generally confined to the tops of canopy trees and high above rivers at the bottom of steep ravines—places where the butterflies receive full exposure to cloud cover and diffuse light. Like brownish morphos, however, the ventral wing surfaces are generally dark shades of reddish-brown, but with reduced ocelli. This feature, in addition to the rather sullen dorsal surface often bordered heavily in brown (as in *theseus,* Fig. 1) suggests a similar compromise between conspicuousness and crypsis resulting from broad host plant specificity encompassing local systems of automimicry as seen for the brownish morphos. However, not being second-growth species like most brownish morphos, a narrower host plant range is predicted for most members of this group.

From these considerations, it is possible that *M. theseus* in Central America represents a gradient of "near-Batesian" to "near-Müllerian" mimic of *M. polyphemus,* which is itself a "near-Müllerian" model, since most individuals of it in local populations are near the unacceptable end of a a palatability spectrum. However, the absence of glossy white morphos in the South American fauna suggests that more relevant selective agents associated with altitudinal distribution of chalky white morphos are guiding the evolutionary history of this lineage. The generally broader geographical distribution of *M. polyphemus* in certain regions of Central America, as contrasted with the very spotty distribution of *M. theseus* (24) is perhaps further indication that mimetic association is unlikely.

As mentioned for certain species *(catenarius, laertes)* by SEITZ (24) and in greater detail very recently by Luiz R. Otero (pers. comms.) for these species, there is very pronounced gregariousness in the chalky white morphos, although data on the life history of *M. theseus* are not yet available. Otero has informed us that *Morpho laertes* lays about 150 eggs on the dorsal surfaces of leaves of the host plant (various Leguminosae), and that the larvae remain together on leaves and branches (of forest trees) until the fourth instar, when they build an elaborate silken nest near the extremities of branches. At this stage, the larvae are very visible, as they cluster in groups (Otero has seen as many as 300 larvae in a group) which hang on the tips of branches. Such behavior is never seen in brownish morphos nor in glossy white morphos. With respect to the latter, it is interesting to point out that *M. polyphemus* has been classified with species of the chalky white group (24). However, there is never any gregarious behavior of larvae in this species, nor are eggs laid in clusters (35). Rather, the oviposition strategy and larval behavior resemble more closely those of certain species of dazzling blue morphos *(M. anaxibia* and *M. menelaus),* perhaps indicating closer phylogenetic relationship with this lineage, as already pointed out with respect to morphological similarities in wing color between *polyphemus* and *cypris.* Studies have not been conducted on the caterpillars of chalky white morphos, and it would be very interesting to determine whether or not larvae possess defense secretions such as those seen for at least one brownish morpho *(peleides)* and *M. polyphemus,* which usually occur singly. Our prediction is that caterpillars of chalky white morphos such as *M. catenarius* and *M. laertes* may possess very weakly developed defense secretions, in response to the gradual reduction in gregarious habit seen in these species which feed on Leguminosae, as contrasted with other members such as *M. hercules* and *M. hecuba* (Table 2). Otero has told us that both of these species feed on various Menispermaceae rather than Leguminosae, and that larval aggregations may contain as many as 800 larvae — far exceeding the numbers seen in the legume-feeding members of this group. Owing to recent studies on phenolic compounds associated with Leguminoseae (14), it is likely that these kinds of host plants offer a greater potentiality for the evolution of defense secretions in *Morpho* larvae and other herbivores that feed on them, than do the Menispermaceae. If we then assume that gregariousness was carried over as a primitive character from the Brassolids, it would then appear that a gradual loss of gregariousness was accompanied by an increase in the efficiency and effectiveness of defense secretions so that selection favored the development of single oviposition and single larvae as important prerequisites for the ecological expansion of the genus *Morpho* into new environments (second-growth plant communities and montane forests). A similar evolutionary trend is clear-cut in the dazzling blue morphos, as pointed out earlier. Within this group, there occur different degrees of cluster oviposition and gregariousness of larvae, ranging from high expression of these phenomena in those species appearing most closely related to the Brassolids, such as *M. aega, M. portis, M. adonis,* and *M. sulkowskyi,* species which also feed mainly upon members of the monocot family Graminae (L. R. Otero, pers. comm.). As one goes up the lineage and examines other species such as *M. anaxibia* and *M. menalaus,* gregariousness has been reduced to the occurrence of triplets and pairs of larvae on individual host plants, although this is never seen in brownish morphos nor in *M. polyphemus.* The trait of larval gregariousness remains, however, well developed in all species of chalky white morphos (Table 2), and until data are obtained on the effectiveness of this behavior of larvae in deterring predatory and parasitic attack, the selective advantage for this retention of the Brassolid character cannot be ascertained. It is also necessary to elucidate qualitative and quantitative differences in phenolic content between host plants in the Menispermaceae for certain species of *Morpho* in this group, and host plants in the Leguminoseae for other species. As indicated by SEITZ (24), species such as *catenarius* and *laertes* inhabit primary-growth forest, and it is probably generally true that the chalky white morphos as a group represent an adaptive strategy in the genus in which the patterns of general ecology and behavior remain similar to those of many Brassolids.

SYNTHESIS

We have attempted to present general patterns in the evolutionary biology of the genus *Morpho,* through correlations between morphological, ecological, and behavioral traits. We have a good record of the wing coloration and brightness patterns in the genus, although our knowledge of ecology and behavior is, at the most, rudimentary. Nevertheless, from the sorts of preliminary data available on certain species from South and Central America, it is evident that there exist markedly different adaptive radiations in the genus. Our thesis has been that there occurred four different adaptive radiations in the genus; two of these were very successful, undergoing extensive speciation and sub-speciation, while the remaining two were rather restricted. These evolutionary patterns are exemplified well by the Central American *Morpho* fauna (Table 1). The dazzling blue morphos represent one major successful radiation in primary-growth lowland wet forests (exemplified by *M. amathonte* and *M. cypris* in Costa Rica) while the brownish morphos (as seen in *M. peleides* and *M. granadensis* in Costa Rica and El Salvador) have primarily undergone adaptive radiation in second-growth plant communities at a wide range of altitudes, but mostly at higher elevations. The two less extensive radiations are shown by *M. theseus* in Costa Rica, a chalky white morpho, which is found in very limited and patchy geographical distributions along the Caribbean slopes of the central Cordillera, and *M. polyphemus,* a glossy white morpho, characteristic of higher elevations where it inhabits both primary-growth (Costa Rica) and secondary-growth (El Salvador) forests. We summarize below some major points regarding these trends.

Many of these adaptive radiations have to do with the fact that morphos are very large butterflies, and therefore are potentially very conspicuous insects for predators; on the one hand, selection has operated in one group (chalky white morphos) towards a retention of important and primitive behavioral characters known for the majority of the supposedly ancestral Brassolids, a group which exploits a strategy of crypsis to escape predation and involving a restriction of adult activity to heavily-shaded forest. The chalky white morphos have undergone a minor adaptive radiation into montane tropical forest where the species are always confined to the primary-growth undisturbed forest for the bulk of their activities related to survivorship and reproduction. In Central America, this radiation is represented by a single species, *Morpho theseus,* which occurs in small isolated populations along the Caribbean slopes of the central Cordillera. Being derived from a relatively ancient lineage, *theseus* represents an unsuccessful evolutionary attempt to radiate adaptively at high elevations, since it exists as only a few subspecies. Like lowland isolated populations of *cypris, theseus* at high elevations is predicted to be subject to either random extinctions or extinctions resulting from habitat destruction by man through agricultural practices.

The dazzling blue morphos, which exhibit a spectrum of ecological and behavioral traits indicating a trend towards greater population dispersal (evolution of single oviposition and non-gregarious larvae) but yet generally confined to lowland primary-growth tropical forests, exploit a strategy of survivorship which involves narrow spectra of larval host plant specificities in which the more highly evolved species feed on very unpalatable plants (mostly Leguminosae and Sapindaceae). In these species, wing brightness in males, maximized by morphological adaptation in the wings for highest reflectance, which in the usual bright direct sunlight at the forest canopy or in forest clearings, makes these butterflies very conspicuous to potential predators. It is speculated that one very highly evolved species of this group, *M. cypris,* represents a lineage of unsuccessful evolution. Populations of this species are small and very isolated, presumably as a result of competitive interactions with another dazzling blue species, *M. amathonte,* which is relatively abundant locally in lowland wet forests. It is *amathonte* which represents the successful evolutionary lineage of the genus in lowland primary-growth forest environments. We predict that *cypris* is subject to become extinct locally more rapidly than *amathonte* in lowland wet forests of Central America, due to massive agricultural practices involved in lumbering and farming. Like the Central American species of *Drosophila* studied by Dobzhansky and his associates, genetic variation in isolated populations of *cypris* will be low, favoring rapid extinction induced by environmental (habitat) changes. We maintain that *M. polyphemus,* which may have evolved in lowlands from *cypris* or *cypris*-like ancestral form, represents a relatively recent ecological expansion into montane primary and second-growth forests. Presumably in response to competitive interactions in lowlands with *amathonte* and *cypris,* this species has escaped from an unsuccessful pattern of habitat exploitation to a successful one by moving up altitudinal gradients. Initially *polyphemus* remained a forest species at higher elevations, but in some regions of Central America (El Salvador), it has subsequently moved into second-growth habitats. Being a relatively recent evolutionary event, the "glossy white morpho" lineage, as exemplified by a single species, *polyphemus,* may undergo further divergence. Comparative studies of the ecological statistics of *M. polyphemus* between Costa Rica and El Salvador should reveal different adaptive ecological strategies; in Costa Rica, the species is predicted to possess life table features characteristic of species well-integrated into tropical communities, while in El Salvador, the same statistics would be skewed towards those of colonizing species — as a response by natural selection towards a new phenotypic norm resulting from environmental alteration due to massive land clearing by man. Costa Rican populations, on the other hand, would be characterized by strong stabilizing selection rather than such disruptive selection. Electrophoretic studies of enzyme systems of *M. polyphemus* in Costa Rica and El Salvador would therefore be extremely interesting to pursue, and important for verification of this idea.

Based on gross morphological features such as general wing shape, it appears that another major successful evolutionary lineage of *Morpho* is represented by the brownish morphos, a very large and diverse group, characterized by a tremendous number of subspecies in South American *(achilles, achillaena)* and Central American *(peleides)* species. The group undoubtedly originated in lowland tropical forests, as some members retain the cryptic features of Brassolids, but the major adaptive strategy has been the invasion of second-growth habitats at many altitudes, and a general geographical expansion into montane forests. A major difference between this group and the glossy white morpho lineage is that the brownish morphos are ancient, having undergone an early successful transition from being species well-integrated in primary-growth forest communities to becoming well-integrated into the less stable second-growth communities. Evolutionary studies of *M. peleides* or *M. achilles* should focus upon an estimation of relative amounts of genetic variability in local populations along altitudinal transects, and between different types of second-growth communities. Furthermore, comparative studies of life table statistics, and the variance about these and related parameters must be made along altitudinal transects and between different plant communities. A more rectangular-shaped survivorship curve is predicted for populations of *M. peleides* in more stable plant communities, while the variance about mean values for ecological statistics such as fecundity, body length, etc., should be lower in these populations. Genetic variability should also be lower. Species such as *peleides* or *achilles* offer ideal opportunities for detailed analysis of the genetic properties of colonizing forms as contrasted to those of non-colonizing forms, in which forms may turn out to be different subspecies. Also of importance would be comparisons of larval host plant specificities among these populations as a means of determining if lowland subspecies are more unacceptable as prey as a whole population (granted the existence of automimicry) than second-growth or montane forest populations. Related to this would be the need to measure subtle differences in wing brightness (reflectance) properties among subspecies from different environments, as an index of relative acceptability as prey; subspecies populations characterized by a higher proportion of brighter individuals would suggest narrower local host plant specialization and greater unacceptability. Studies are now in progress to compare reflectance properties of the wings of *M. peleides* from specimens collected along altitudinal transects from Puerto Viejo (98 m) to Cuesta Angel (1000 m) in Costa Rica, as a preliminary step in this direction. Right now, we know that qualitatively wings of male *peleides* from Puerto Viejo appear brighter than wings of *peleides* from Cuesta Angel. Such measurements should also be made for *achilles* in Brazil.

Species of brownish morphos are predicted to be relatively insensitive to selection pressures favoring local extinctions of breeding populations or demes. High genetic variability, broad larval host plant specificity, high mean adult population density, and high adult vagility are characteristics of the brownish morphos that permit successful colonizing episodes in response to habitat destruction induced by climatic factors (mud slides, river floods) or by man (road constructions, agricultural practices, etc.). Like the successfully adapted dazzling blue morphos in lowland wet primary-growth forests, the brownish morphos of second-growth wet forests at any given altitude are genetically and phenotypically adapted to some forms of habitat alteration, and perhaps even more so than dazzling blue morphos. A major difference in adaptive strategy between the two groups may be that dazzling blue morphos are "K strategists" while brownish morphos are "*r* strategists". Species in very stable communities are predicted to experience Strong K selection while species in less stable communities experience *r* selection. Such predictions are testable with species such as *peleides* and *amathonte* since populations of both butterflies are readily accessible, permitting estimations of developmental time, age-specific fecundity (m_X), and age-specific mortality (l_X).

It is realized that within the four groups originally postulated in this paper, there will exist differences among member species for the various ecological and behavioral traits discussed. It is our belief that fine-analysis comparison of these differences, rather than relying solely upon morphological components of the phenotype, will provide a more comprehensive picture of the evolutionary biology of *Morpho*. Studies should emphasize: (a) detailed documentation of local spectrum of host plant acceptance, (b) the relative unacceptability of larvae and adults reared on the various host plants of a local population, (c) measurement of the variance about mean egg cluster size and mean size of groups of gregarious larvae within local populations of a subspecies and among different populations of the same subspecies and different subspecies, (d) further detailed study of patterns of daily movement of individuals in the environment and precisely how they relate to courtship and population dispersion, (e) estimation of rates of parasitism and predation on eggs, larvae, and adults among different populations of the same subspecies at different altitudes or varying degrees of plant succession, (f) estimations of the amount of genetic variability in different populations of the same subspecies and between different subspecies, and (g) laboratory breeding studies on selected species such as *Morpho peleides* and *M. achilles*, to elucidate the genetic mechanisms underlying subspecies-status determination, zones of hybridization in nature, or zones of gene introgression. Studies of this sort have been profitable in other species. Experiments on the genetics of *Heliconius melpomene* (TURNER, 28) have been useful in elucidating mechanisms of genetic variability as a function of geographical distribution of populations; similar analyses with species such as *M. peleides* could also be pursued with like success. These studies have been initiated with *M. peleides* and *M. polyphemus* in Costa Rica and El Salvador since these species appear to have undergone major ecological expansions (*peleides*) or are still in the process of doing so (*polyphemus*). Such information, however, is needed for many species of *Morpho*, if the predictions discussed above and summarized in Tables 1 and 2 are to be confirmed. As a genus, the morphos offer an excellent opportunity to analyze mechanisms of adaptive (ecological) radiation that are characteristic of relatively few tropical groups of butterflies, with perhaps the exception of the genus *Parides* and selected genera of Satyrinae.

We would hope that our approach with *Morpho* butterflies could be extended to studies concerning ecological expansions in other groups of tropical organisms. Since different ecological expansions within a taxonomic group result from extensive or recent evolutionary events involving adaptations of different members of the group to different kinds of terrestrial habitats (i.e., along an altitudinal gradient, or between different communities at a given altitude) it is useful to examine the various character states of morphological, behavioral, and ecological traits in representative species within these habitats. As we have attempted to do here with *Morpho*, it should then be possible to make some predictions about the incidence of successful and unsuccessful evolutionary adaptive radiations which can be accounted for in terms of the traits studied. We now propose to return to the field to examine further these traits in Central American *Morpho*, as an approach to testing predictions (Table 3) about those aspects of phenotype exhibited by different species in various tropical environments.

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RESUMEN

Se estudió caracteres morfológicos, de comportamiento y ecológicos de especies centro y sudamericanas de mariposas *Morpho* para tratar de explicar la distribución geográfica y ecológica actual del género en América Central. El enfoque principal fue sobre las radiaciones adaptativas, exitosas o no, de diferentes grupos de especies en distintas alturas y en comunidades vegetales primarias y secundarias. Se postula que existen dos radiaciones adaptativas exitosas mayores de *Morpho* en Centro América caracterizadas en la actualidad por tres especies: *M. granadensis* y *M. peleides* hacia comunidades secundarias en bosques de bajura y del montano, y *M. amathonte* hacia bosques primarios de bajura. Las tres especies tienen territorios amplios en donde existen sus habitats, todas son comunes localmente y por lo menos dos de ellas *(granadensis* y *peleides)* muestran altos niveles de subespeciación y de variación. Los fracasos de radiación adaptativa, caracterizados por poblaciones pequeñas aisladas y por baja subespeciación, se evidencian en América Central por *M. cypris* en bosques primarios de bajura y por *M. theseus* en bosques primarios del montano. *Morpho polyphemus* representa una posible transición entre una radiación adaptativa fracasada en bosques del montano y una radiación adaptativa exitosa en bosques de bajura y del montano.

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Fig. 1. Top row, left to right: *Morpho amathonte centralis* (♂), "dazzling blue morpho"; *Morpho polyphemus polyphemus* (♂), "glossy white morpho". Bottom row, from left to right: *Morpho peleides limpida* (♂), "brownish morpho"; *Morpho theseus theseus* (♂), "chalky-white morpho". The butterflies are from various regions in Costa Rica.