

location. The significant question is whether these butterflies rest individually or clumped in aggregations.

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NATURAL HISTORY NOTES FOR SOME *HAMADRYAS* BUTTERFLIES
(NYMPHALIDAE: NYMPHALINAE; AEGERONINI) IN NORTHWESTERN
COSTA RICA DURING THE TROPICAL DRY SEASON

The relatively small cluster of species belonging to the nymphaline genus *Hamadryas* are well known as "calicoes" or "crackers" in the adult stage throughout much of Central America, Mexico, and South America. The medium-sized gray-and-white speckled butterflies are pugnacious, fast-flying insects that commonly perch on the trunks of trees during the daytime, head downwards, and with the wings held pressed down in the open position. Their fast aerial antics coupled with loud clicking noises evident in both sexes, and often involving attack approaches to "intruders" into their areas, have made them the subject of behavioral studies (e.g., Ross, 1963, *J. Res. Lepid.* 2:241-246). As a group, the caterpillars feed on Euphorbiaceae, particularly vines and shrubby plants of the genus *Dalechampia* (e.g., Young, 1974, *Z. Angew. Entomol.* 76:380-393; Muysshondt & Muysshondt, Jr., 1975a, *J. New York Entomol. Soc.* 83:157-169; 1975b, *J. New York Entomol. Soc.* 83:170-180; 1975c, *J. New York Entomol. Soc.* 83:181-191; Jenkins, 1983, *Bull. Allyn Mus.* 81:1-146) and may function as significant selective agents in the evolution of herbivore resistance in these plants (Armbruster, 1982, *Amer. J. Bot.* 69:1429-1440). Adult butterflies are typically associated with open pastures and borders of dense vegetation (Ross, 1964, *J. Res. Lepid.* 18:11-26; 1967, *J. Res. Lepid.* 18:11-26; 1967, *J. Res. Lepid.* 15:109-128; Monroe et al., 1967, *J. Lepid. Soc.* 21:185-197). Because some species of *Hamadryas* occur in the seasonal tropical dry forest zones of Central America, they offer the chance to study the impact of tropical seasonality upon their natural history. In this note we report such preliminary field studies from the lowland tropical dry forest zone of northwestern Costa Rica as performed during the dry season. Herein, we describe some hitherto unreported features of adult behavior, including nocturnal perching relative to daytime perching, and evidence that, although females are mated during this period, they appear to be in a state of reproductive diapause.

From 2-4 March 1984 we studied and collected adult *Hamadryas* from these two localities: (a) about 1.5 km south of Liberia (10°40'N, 85°40'W), Guanacaste Province and along the Pan American Highway, and (b) "Barranca Site" (Orlans, 1969, *Ecology* 50:783-801) about 6 km from Miramar (10°06'N, 84°44'W), Puntarenas Province. Both localities fall within the region of lowland tropical dry forest and experience a completely dry (no rainfall) season generally between December and May each year. Within a wide rectangular roadside area (approx. 50 m × 100 m) at the Liberia site, we studied the abundance and habits of adult *Hamadryas* on several mature forest canopy trees, mostly *Guazuma ulmifolia* Lam (Sterculiaceae). Approximately 75% of this area was covered by a dense patch of disturbed forest, consisting chiefly of a *Guazuma* "canopy" and fairly evergreen understory consisting of various Leguminosae, Flacourtiaceae, and other small trees and shrubs in varying degrees of "leafing out" at the time. We examined the distribution of adult *Hamadryas* perching on tree trunks within the forest patch and along its borders at various times of the day and night. As it was quickly apparent that the butterflies were most numerous along the strip of shade trees between the forest patch and the highway (Fig. 1), we concentrated our observations to that area which

contained eight mature *G. ulmifolia*, one *Enterolobium cyclocarpum* Donn. Smith. (Leguminosae) and two palms (unidentified). We observed the occurrence of *Hamadryas* adults on the trunks of these and other trees during the daytime and also on two evenings; daytime observations were made intermittently from about 0800 and 1800 h on the two days. Evening or nocturnal observations were limited to 2000 to 2200 h. We searched tree trunks and foliage for resting butterflies at night, using head lamps and flashlights. On 3 March, we studied the movement of butterflies from tree trunks to other perching sites at 1700 to 1800 h.

Potential adult food sources were noted as well as the availability of *Dalechampia* within the immediate vicinity (the forest patch) to determine the presence of immature stages. On the first night of study (2 March), we collected a series of adults for species vouchers, and during the day we made every attempt to recognize different "morpho-species" of adults and later matched vouchers with these field observations. We measured air temperature patterns in both shaded and exposed areas during the late morning, as well as wind strengths. To do the latter, we determined the degree to which the bag of a standard insect aerial net would be inflated (held horizontally) at the edge of the forest acting as a wind break and also in the adjacent pasture. We did this to determine a possible relationship between adult perching sites and protection from the strong wind gusts characteristic of the Guanacaste dry season.

Three piles of rotting bananas were placed on the ground at the "Barranca Site" locality, a patch of semi-deciduous forest; these baits were placed along the foot path and the upper or southern end of this forest patch to attract adult *Hamadryas*. These three baits were scattered at 50–100 m intervals along the train, and the first one was placed at the base of a large *Samanea saman* (Leguminosae) tree, which is located about 10 m from a small grove of *G. ulmifolia* trees. The baits were distributed at about noon on 2 March and reexamined for butterflies between 1400–1600 h on 4 March. Our purpose was to determine the *Hamadryas* species active here to compare with Liberia specimens, and to collect females for evidence of mating and reproductive condition.

Adult female butterflies were stored in glassine envelopes and placed in a freezer upon return to Milwaukee a few days after the field work. The butterflies were then thawed and examined with a dissecting microscope to determine (a) the presence of spermatophores and mating plugs, and (b) the degree of development of ovary tissues. The number of ova, immature and mature, were counted. Species determinations were made following the keys of Jenkins (op. cit.).

Notes were taken on the presence and activity of other Papilionoidea at both localities to compare with *Hamadryas*.

At about 2100 h on 2 March we collected five *Hamadryas guatemalena guatemalena* (Bates), and two *H. glauconome glauconome* (Bates) and one *H. feronia farinulenta* from the foliage of two adjacent trees along the front edge of the forest patch facing the highway. Other butterflies collected perching in the same foliage included *Callicore pitheas* (Latreille) and *Opsiphanes cassina fabricii* (Boisduval) (Brassolidae). Unlike daytime perching on tree trunks, nocturnally perching *Hamadryas* are positioned on the undersides of leaves and with their wings tightly folded. The same is true for other butterflies found perching on foliage at night (see also Young, 1979, J. Lepid. Soc. 33: 58–60). In some instances, *Hamadryas* adults at night could be collected using fingers rather than a net.

On the following afternoon, we documented the movement of *Hamadryas* from tree trunk perching sites to nearby foliage for nocturnal roosting. Between 1741 and 1756 h, we observed a total of 13 butterflies (three species: *H. guatemalena guatemalena*, *H. glauconome glauconome* and *H. feronia farinulenta*) fly into a single evergreen bush within 3–5 m of nearby *G. ulmifolia* trees used as daytime perching sites. At approximately 1 to 2 minute intervals, 1–2 butterflies fluttered into the foliage from the surrounding area, and by 1758 h, all 13 individuals were perched on the undersides of leaves with wings closed, and all within 15 cm to 1.0 m of one another in the bush. Throughout the study period, the weather was hot, sunny and dry. During the dusk settling process, arrivals of some individuals resulted in others being temporarily disturbed, flying off and

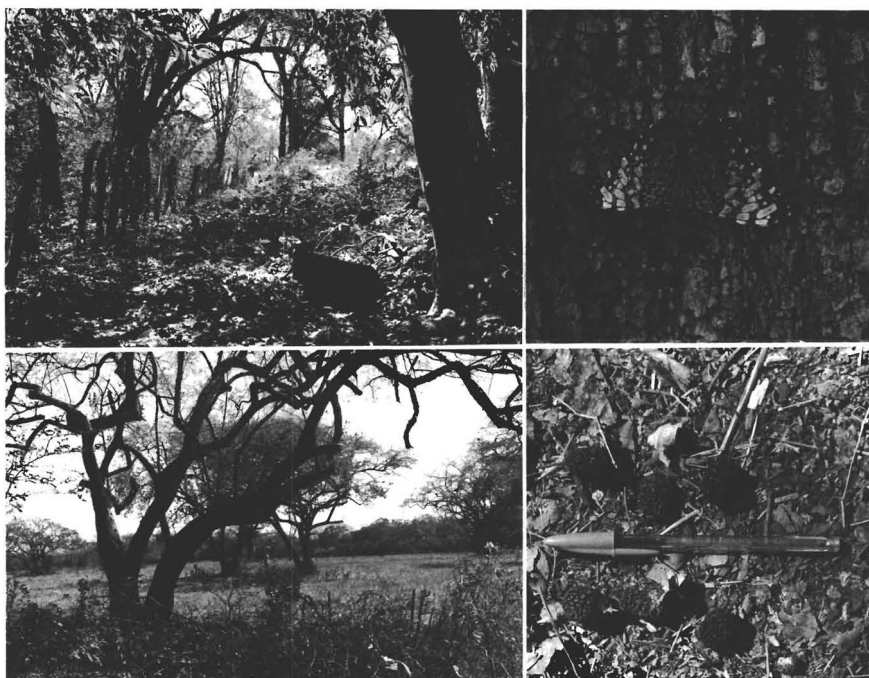


FIG. 1. Clockwise, from upper left photograph: the western edge of the forest habitat at the Liberia locality—*Hamadryas* was commonly found perching on the trunks of the trees to the right during the day and on the foliage to the left (4 March 1984); *H. guatemalena* resting on the trunk of a tree at the Liberia locality; *Guazuma ulmifolia* fruits on the ground; *G. ulmifolia* trees in the open pasture immediately south of the forest patch at the Liberia locality (also 4 March 1984).

eventually returning. A check later that evening (about 2030 h) revealed no further additions. Butterflies did not perch on foliage during the daytime.

A search for *Hamadryas* butterflies on tree trunks throughout the study site at Liberia (4 March at about 0900 h) revealed none associated with trees within the forest, nor any along trees bordering the eastern, northern, and southern boundaries of this patch; all butterflies were found on a few trees along the western border of the patch. Of eight *G. ulmifolia* trees in this area, only three had one or more *Hamadryas* perching on them during the day. There was almost an equal number of both sexes, judging from field observations and collections made, but one species, *H. guatemalena*, was more commonly encountered than others at both localities (Table 1). Most of these butterflies appeared to be "fresh" in terms of the wing condition, and all but one female was mated (Table 1). Interestingly, only one species, *H. guatemalena*, was found at both localities, with an additional four species being distinct between them (Table 1).

We could not detect any species-specific differences in daytime or nocturnal perching behavior at Liberia. It appeared that all species were responding to prevailing environmental conditions in the same manner. Mid-morning measurements (1000 to 1030 h on 3 March) of air temperature in the shade at a *G. ulmifolia* tree frequently used for perching by *Hamadryas* and another individual of the same tree a few meters away and in direct sunlight revealed no differences (31.0°C at both trees at 1000 h and 30.6°C and

TABLE 1. Sex ratios, relative wing condition, and reproductive states for small samples of adult *Hamadryas* species at two localities in northwestern Costa Rica during the tropical dry season.*

| Date(s) | Species | No. of adults | | | Wing condition** | Reproductive state |
|-----------------------------|--|---------------|--------|-------|------------------|--------------------|
| | | Male | Female | Total | | |
| “Liberia, Guanacaste” | | | | | | |
| 2–4 March 1984 | <i>H. guatemalena</i> | 4 | 1 | 5 | 2mF, 2mI, 1fF | mated |
| | <i>guatemalena</i> (Bates) | | | | | |
| | <i>H. glauconome</i> | 2 | 0 | 2 | 2mF | — |
| | <i>glauconome</i> (Bates) | | | | | |
| | <i>H. feronia farinulenta</i> (Fruhst.) | 1 | 0 | 1 | 1mF | — |
| “Barranca Site, Puntarenas” | | | | | | |
| 4 March 1984 | <i>H. guatemalena</i> | 0 | 2 | 2 | 2fF | mated; |
| | <i>guatemalena</i> (Bates) | | | | | mated |
| | <i>H. februa ferentina</i> (Godart) | 0 | 1 | 1 | 1fF | unmated |
| | <i>H. iphthime iphthime</i> (Bates) | 0 | 1 | 1 | 1fF | mated |

Total species (both localities): 5

Total individuals & overall sex ratio: 7 males + 5 females = 12

* Counts were made of adult butterflies found perched on trunks, branches, and leaves of trees at the study sites. Other species present at the "Liberia" locality trees were: *Callicore pitheas* (Latreille), *Eunica malvina* (Bates), *Siderone marthesia* (Cramer), and *Opsiphanes cassina fabricii* (Boisduval). Reproductive states were examined for female butterflies only.

** Lowercase letters refer to sex (m = male, f = female) while uppercase letters designate wing condition: F = fresh, I = intermediate-worn.

30.8°C for exposed and shaded trees, respectively, at 1030 h). We did discover that wind gusts quickly inflated the bag of the aerial insect net along the open pasture area immediately adjacent to the forest patch, but the bag remained almost completely deflated when positioned along the western edge of the forest at the point where butterflies were perching on tree trunks (tests performed 0930-1000 h on 3 March). This observation suggests a wind-sheltering factor in the choice of tree trunks by *Hamadryas*.

Counts of freshly fallen, sweet-smelling, *G. ulmifolia* fruits in four different one-by-one meter plots gave the following results: 70 and 73 fruits for two adjacent trees along the shaded western edge of the forest patch and 25 and 15 fruits each for two trees in the open pasture south of the forest patch. Since some butterflies in this region of Costa Rica feed on fallen *G. ulmifolia* fruits (e.g., Young, 1975, Rev. Biol. Trop. 23:101-123), we attempted to observe possible feeding by *Hamadryas* on these fruits at the Liberia locality, but this behavior was not observed. We searched for evidence of adult *Hamadryas* feeding on these fruits, fresh cattle dung, and sap flows at the Liberia locality, but none was seen in spite of checking at various hours of the day. Most of these observations took place after 0830 h and we might have, therefore, missed an early morning feeding period. Of four *Hamadryas* observed near one of the banana baits at the Barranca Site, one of these was found feeding on the bait (1400 h, 4 March) along with several *Caligo memnon* Felder; three of the *Hamadryas* were perched on the *S. saman* tree immediately behind the bait. No *Hamadryas* were found here on either of the two remaining baits or on *G. ulmifolia* fallen fruits nearby.

Of the five female specimens of *Hamadryas* collected for examination of reproductive condition, only one individual of *H. guatemalena* had a single mature (sculpted surface) egg and all others either had no ova at all or immature ova, in spite of (a) appearing in relatively "fresh" wing condition and (b) with one exception, being mated as evidenced by the presence of single spermatophore (Table 2). The spermatophore found in the

TABLE 2. Evidence for a lack of female reproductive activity (egg production) in *Hamadryas* species in northwestern Costa Rica during the tropical dry season.

| Species* | Female no. | Condition of ovary | Spermatophore** |
|-------------------------------------|------------|-----------------------------|------------------------------------|
| <i>H. guatemalena</i> | 1 | no ova | one present, "fresh" (mated) |
| <i>guatemalena</i> (Bates) | 2 | no ova | one present, "fresh" (mated) |
| | 3 | one near full size egg only | one present, broken, "old" (mated) |
| <i>H. februa ferentina</i> (Godart) | 1 | no ova | none (unmated) |
| <i>H. iphthime iphthime</i> (Bates) | 1 | four immature ova | one present, "fresh" (mated) |

* With the exception of one female of *H. guatemalena*, all of these butterflies were collected at the "Barranca Site" locality.

** "Fresh" spermatophores appeared full and when pierced, exuded a milky fluid, and were intact within the bursae copulatrix; "old" spermatophore appears collapsed and fragmented.

individual with the single mature egg appeared "old" since it was easily fragmented during the dissection, whereas, other spermatophores appeared "fresh" (Table 2).

Our data, while preliminary and based upon small sample size, does point out some interesting new information about the natural history of *Hamadryas* in lowland tropical dry forest during the dry season: (1) occurrence of individual species may vary considerably over relatively small distances (e.g., 40 km); (2) behavioral posturing associated with nocturnal perching is very different from that of daytime perching, both in the site of perching and the posture of wings; (3) the choice of both daytime and nocturnal perching sites may be determined in part by the location of trees and foliage in wind-sheltered places and having little or nothing to do with thermoregulation in response to dryness; (4) by the middle of the lengthy dry season there may be little or no reproductive activity as indicated by the absence of mature ova in most female specimens examined; (5) adults active at or near the middle of the dry season may represent the final "wave" of adults to eclose during this season as seen by their "fresh" wing condition and that these individuals do mate; and (6) there may be little or no adult feeding at this time, and little or no egg placement as well. Young (op. cit.) studied the life cycle of *H. februa* at the Barranca Site early into the dry season (December) and observed egg placement and successful larval development on *Dalechampia*, which was still evergreen at this time. He might have been studying the immature stages of a crop of fresh adults that would be active later in the dry season at this locality. Ehrlich and Ehrlich (1978, J. Kansas Entomol. Soc. 51:666-697) collected a single female of *H. feronia* which had thirteen ova, a figure in sharp contrast with the ova-less females found in our study. We interpret this difference to highlight the lack of reproductive activity in these butterflies, as seen in our sample, during the latter half of the tropical dry forest lengthy dry season. Spermatophores present in these butterflies at this time appeared fresh (i.e., filled with milky white fluid) and perhaps are used to fertilize ova that may develop at the end of the dry season and early into the rainy season. As we did not find larval food plants at the Liberia locality and did not check for them at the Barranca Site, we can only tentatively speculate that they were in short supply at this time of the year. We suggest that *Hamadryas* undergo a reproductive diapause in ovarian development during the latter half of the dry season and that the presence of fresh spermatophores at this time is an adaptation to facilitate egg maturation and egg placement when the rainy season begins. The observed absence of mating plugs suggests that these females may mate again, perhaps at the end of the dry season or early into the rainy season, if they survive. Butterflies thriving in open areas and at the edges of forest habitats in the tropics may necessarily experience such cessations in breeding in response to diminished resources for immature stages. The association of *Hamadryas* with such habitats is well known (e.g., Ross, 1976, op. cit.; Jenkins, 1983, op. cit.; Schwartz, 1983, Mus. Nac. Hist. Nat.

Santo Domingo, 69 pp.). Adult butterfly populations in the seasonal tropics generally decline as the dry season advances, and there is less reproductive activity at this time, both in the New World and Old World tropics (e.g., Young, 1981, Oct. Oecol. Ecol. Gener. 2:17-30; Spitzer, 1983, J. Res. Lepid. 22:126-130).

Declines in butterfly populations with the dry season may reflect contracting supplies of larval food (Spitzer, 1983, op. cit.), and reproductive activity may be restored as deciduous larval food plants produce tender, new meristems in the latter half of the dry season (Young, 1983, J. Lepid. Soc. 37:313-317). In one forest patch along the Pan American Highway between Canas and Liberia, we observed the moth *Haemaorrhagia* (Sphingidae) carefully placing eggs singly on the small (2-5 mm long) folded leaf meristems of an unidentified understory tree near dusk (2 March). Adults of many butterfly species were seen at the Barranca Site at this time, including: *Morpho peleides* Kollar, *Caligo memnon* Felder, *Memphis morvus boisduvali* Comstock, *Consul fabius* Doubleday, *Siproeta stelenes* Fruhst., *Zaretis itys* Cramer, *Taygetis andromeda* Cramer, *Philaethria dido* Linnaeus, *Parides arcas mylotes* Bates, *Battus polydamas* Linnaeus, and *Papilio anchisiades idaeus* Fabricius. Many plant species at this locality have small meristems at this time, and some butterfly species selectively oviposit on these tissues. For example, we observed *Itaballia demophile calydonia* Boisduval carefully placing eggs singly on very fresh leaf meristems of *Capparis* sp. (Capparidaceae) at 1530 h on 4 March. Cuttings of meristem stem tissues of this plant species quickly wither, even when confined to tightly closed plastic bags, whereas, cuttings of older stems do not wither as fast. We interpret these observations to mean that considerable moisture stress is operative on butterfly food plants at this time and that new meristems may be a very limited resource for egg placement in various plant groups present.

Our data suggest that *Hamadryas* adults devote considerable time daily to perching on tree trunks in sheltered places. Many insects living in moisture-stressed habitats carefully position themselves to minimize direct exposure to sustained dryness and related ambient factors (e.g., Egwuatu, 1980, Z. Angew. Entomol. 90:347-354; Toms, 1981, Zool. Zh. (U.S.S.R.) 60:1486-1494; Shelly, 1982, Physiol. Zool. 55:335-343; Gillis & Possai, 1983, Ecol. Entomol. 8:155-161; Findlay et al., 1983, Ecol. Entomol. 8:145-153; Chappell, 1983, Anim. Behav. 31:1088-1093; Shiffer, 1983, J. Med. Entomol. 20:365-370). Often-times, an insect species in a particular habitat will exhibit strong diurnal changes in distribution in response to day-night cycles of both temperature and illuminance (e.g., Van Etten, 1982, Entomol. Exp. Appl. 32:38-45; Parker, 1982, Amer. Midl. Nat. 107: 228-237). The nymphalid butterfly *Anartia fatima* Fabricius forms loose "aggregations" of adults in wind-sheltered bushes for nocturnal perching during the Guanacaste dry season (Young, 1979, op. cit.). The observed tendency for adult *Hamadryas* to perch both day and night on the wind-sheltered edge of a forest patch may reflect a concentration of "nuclear" adult populations around such places during the dry season. Mediterranean fruit flies are present in higher densities in traps in dry areas than in wet areas in the Hawaiian Islands (Vargas et al., 1983, Environ. Entomol. 12:303-310). The same species of insect may selectively choose different plant parts as perching sites at different times of the diurnal cycle, as witnessed in our study. Tsetse flies in Africa perch on woody plant parts in the day and on leaves at night (Turner, 1980, Insect Appl. Sci. 1:15-21).

Our data clearly suggest a tenacity of *Hamadryas* to forest sites in the seasonal tropics, an adaptive response, we suggest, to increasing the survival of small populations of diapausing adults in protected places until the rainy season begins and larval food plants leaf out. Many Euphorbiaceae exhibit marked seasonal cycles in vegetative growth in the tropics (Lieberman, 1982, J. Ecol. 70:791-806). And while dry season weather conditions may have adverse effects on egg-laying activity in butterflies (e.g., Zalucki, Res. Popul. Ecol. 23:318-327), we suspect that severe larval food plant availability is the prime factor selecting for dry season diapause in adult *Hamadryas* during the later phases of the dry season in this region of Costa Rica. We do not extend these predictions to other, i.e., less seasonal, regions of Central America where these butterflies also occur. "Fresh" but mated female *Hamadryas* may exhibit a preference for staying in and near forest patches during the dry season and may move away from these sites in search of

oviposition sites when older. Older, mated tsetse flies exhibit different habitat preferences from new females in the Ivory Coast (e.g., Gouteux, 1982, Cah. Orstom. Ser. Entomol. Med. Parasitol. 20:41–61). In short, we might have missed finding older female *Hamadryas* (with “worn” wings) since our census program was very limited. But, both “fresh” and “worn” males and females of *Morpho peleides* Kollar (Morphidae) exhibit confined movements in the Barranca Site forest throughout the dry season (Young & Thomason, 1974, op. cit.).

We were surprised to find no evidence of adult feeding in our brief study, with the exception of observing one adult on the banana bait at the Barranca Site. While these butterflies are known to feed on sweet smelling rotting fruits (e.g., Schwartz, 1983, op. cit.) as well as on tree sap (Ross, 1976, op. cit.) and horse dung (Jenkins, 1983, op. cit.), we did not observe feeding on naturally occurring food sources. The cattle trail that runs to one side of the trees along the highway had piles of fresh dung (cattle and horse). Jenkins (1983, op. cit.) suggests a preference for horse dung over cattle dung by these butterflies. Whether or not there is a cessation of adult feeding in the dry season physiologically linked to a probable reproductive diapause, remains to be studied. Subsequent to this study, one of us (A.M.Y.) observed *H. amphinome mexicana* (Lucas) feeding on freshly fallen “guava” fruits at “Finca La Tirimbina,” near La Virgen (10°23'N, 84°07'W; 220 m), Sarapiquí District, Costa Rica on 2–4 August 1984. Several butterflies were seen inserting their probosci into small wounds in the fruits (1100–1400 h).

Because shaded pockets of forest in highly seasonal tropical localities are refugia for many animals during the dry season, predation upon adult *Hamadryas* may be exceedingly high at these times, further selecting for avoidance of feeding, particularly on the ground. Lizards and birds figure prominently as predators on adult *Hamadryas* (Jenkins, 1983, op. cit.). Different types of predators, attacking different life stages, may act at different seasons to exploit *Hamadryas* populations. If predation on adults is high during the dry season, it might be lower in the rainy season and replaced at these times by increased mortality of immature stages. In the seasonal tropics, some insect populations are “regulated” by varying sets of mortality factors associated with seasonality (e.g., Page, 1980, Bull. Entomol. Res. 70:621–633). At times of the year when both larval and adult food resources are abundant, immature stages of *Hamadryas* populations may build up most intensely in the vicinity of adult resources, as suggested by some temperate zone butterfly studies (Murphy, 1983, Environ. Entomol. 12:463–466). When this occurs, *Hamadryas* caterpillars may become a major herbivore of *Dalechampia* situated near adult feeding sites (Armbruster, 1982, op. cit.). However, such an interaction is predicted, on the basis of our preliminary results, to be inoperative during the latter half of the dry season in the lowlands of northwestern Costa Rica.

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DONATION OF BLANCHARD LEPIDOPTERA COLLECTION TO THE SMITHSONIAN INSTITUTION

Until recently, few regions of comparable diversity in the United States had been as little surveyed for Lepidoptera as the State of Texas. Thus, it is with considerable gratitude and respect that the Smithsonian Institution acknowledges the donation of the largest and finest prepared collection of Lepidoptera ever assembled from this region, as well as the total accomplishments of Mr. André Blanchard, the man responsible.