GENERAL NOTES

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NATURAL HISTORY NOTES ON *ASTRAPTES* AND *URBANUS* (HESPERIIDAE) IN COSTA RICA

The close evolutionary affinity between *Astraptes* and *Urbanus* skippers (Hesperiidae) as members of the "*Urbanus* group" within the Pyrginae (Evans, 1952, Catalogue of the American Hesperiidae. Part II, British Museum of Natural History, London, 178 pp.) suggests similarities in the comparative biology of immature stages among representative species in both genera. For example, published larval food plant records for both genera include Leguminosae, and *Astraptes* has only been found feeding on members of this family (e.g., Howe, 1975, The butterflies of North America, Doubleday & Co., New York, 591 pp.; Kendall, 1976, Bull. Allyn Mus. No. 39, 9 pp.). While the majority of *Urbanus* species are legume-feeders as caterpillars, a handful of species are grass-feeders (Howe, op. cit.). Further field studies on the natural history of selected species in both genera may either confirm existing patterns of larval food plant patterns or augment them with records involving yet other families of dicotyledonous plants. It is evident that, within the Hesperiidae, tropical genera and species have undergone considerable evolutionary divergence in terms of larval food plants, with ten or more distinct food plant families known for some regions of the Neotropics (e.g., Kendall, op. cit.). In this note I summarize life cycle and larval food plant notes for *A. fulgerator* (Walch) in Costa Rica and make some brief comparisons with similar data on *U. proteus* (Linnaeus) from the same or similar localities within the country. Information on egg laying behavior is also presented. Two new larval food plant families for *A. fulgerator* are presented. The comparison of larval biology between these two genera was prompted by the striking differences in larval appearance between them, even when both are found on legume food plants and suggesting very different strategies of larval defense against visually hunting predators.

Life cycle and related natural history notes on *A. fulgerator* and *U. proteus* were accumulated intermittently over more than ten years at the following Costa Rican localities: "Bajo La Hondura" near Coronado (10°03'N, 84°00'W; 900 m elev.), San Jose Province (1972–1973); "Cuesta Angel" near Cariblanco (10°16'N, 84°10'W; 1000 m elev.), Heredia Province (1973); "Finca La Tigra" near La Virgen (10°23'N, 84°07'W; 220 m elev.), Sarapiqui District in Heredia Province (1982); "Finca La Lola" near Siquirres (10°06'N, 83°30'W; 80 m elev.), Limon Province (1983); "San Rafael de Ojo de Agua" near Ojo de Agua (8°41'N, 83°28'W; 600 m elev.), Alajuela Province (1984); "Barranca Forest" near Puntarenas (9°30'N, 84°35'W; 50 m elev.), Puntarenas Province (1984). These localities encompass a broad range of vegetational formations, from lowland to montane tropical wet forest, and including highly seasonal regions (Ojo de Agua and Barranca). All observations on egg laying behavior and collections of early stages were made in highly disturbed secondary habitats, including the borders of forest (La Tigra), forest remnants (Ojo de Agua and Barranca), and in a cacao plantation (La Lola). Immature stages were often reared through adulthood by confining eggs or caterpillars in tightly closed clear plastic bags containing fresh cuttings of the food plant. Food plant voucher specimens were collected for identification in all instances. Notes are also included for an undetermined species of *Astraptes*.

Urbanus proteus Natural History

Various authors have discussed the life cycle of this common skipper, and in this note I highlight only certain aspects of natural history relevant to a discussion of larval food plant exploitation and comparative behavior of immature stages between this species and *A. fulgerator*. Eggs (each about 1.8 mm dia., white to pale yellow with vertical grooves; spherical with flattened top) are deposited singly on ventral surface of mature

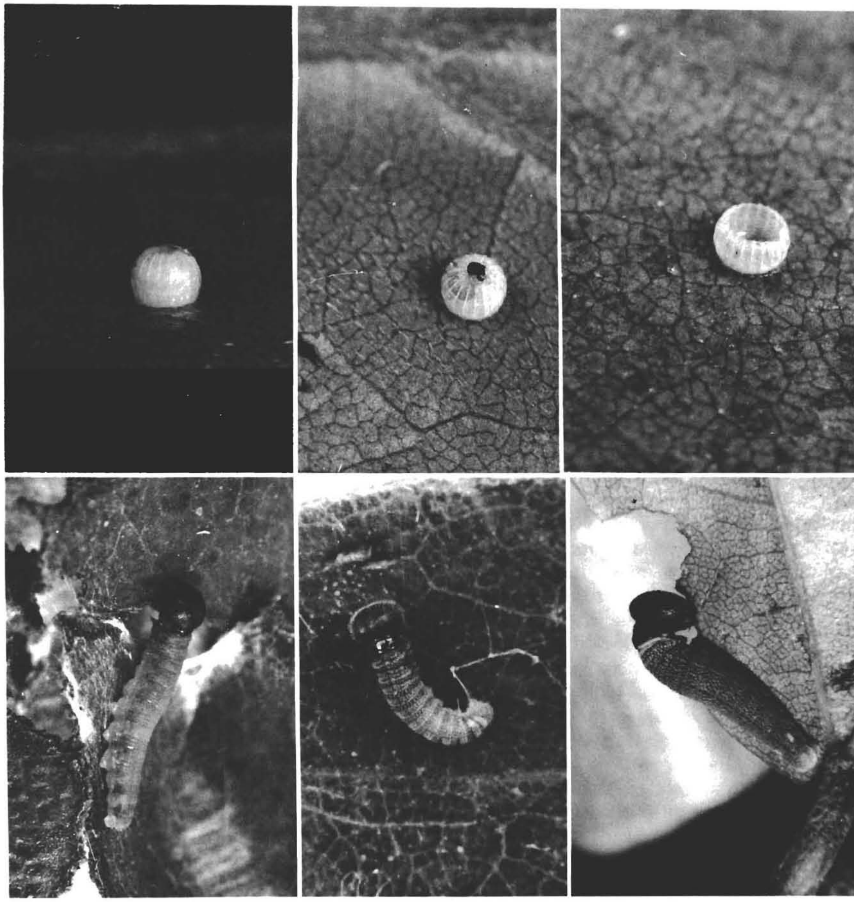

FIG. 1. Egg, first-instar, and second-instar caterpillars of *Urbanus proteus* in Costa Rica. Upper panel, from left to right: recently deposited egg, lateral view; egg in the process of hatching; egg shell after hatching. Bottom panel, left to right: first-instar about 10 minutes after hatching; first-instar constructing shelter (note silk threads); second-instar feeding at the edge of a mature leaf of *Mucuna* sp. (Leguminosae).

leaves of *Mucuna* spp. (Leguminosae), and only the top of the egg shell is eaten during the hatching process (Fig. 1). The first and second instar caterpillars construct a shelter in which to be concealed by folding over an irregularly shaped fragment of leaf along the leaf edge (Fig. 1). The caterpillar lines both surfaces of this structure with a loose network of silk and generally perches on the underside of the "roof" portion of the shelter (Fig. 2). Although initially a pale reddish brown, the caterpillar generally retains the same basic body color pattern throughout all instars: head capsule markedly bi-lobed vertically and shiny dark brown; neck "collar" red-brown above and red below (lateral-ventral flanges); body light green with "speckled" appearance and sparse pubescence of short, soft hairs (white); body sometimes appearing orange-green and with one pair of longitudinal orange lines running the length of the body; next-to-last abdominal segment with one pair of large orange blotches dorso-laterally; anal plate dark greenish brown

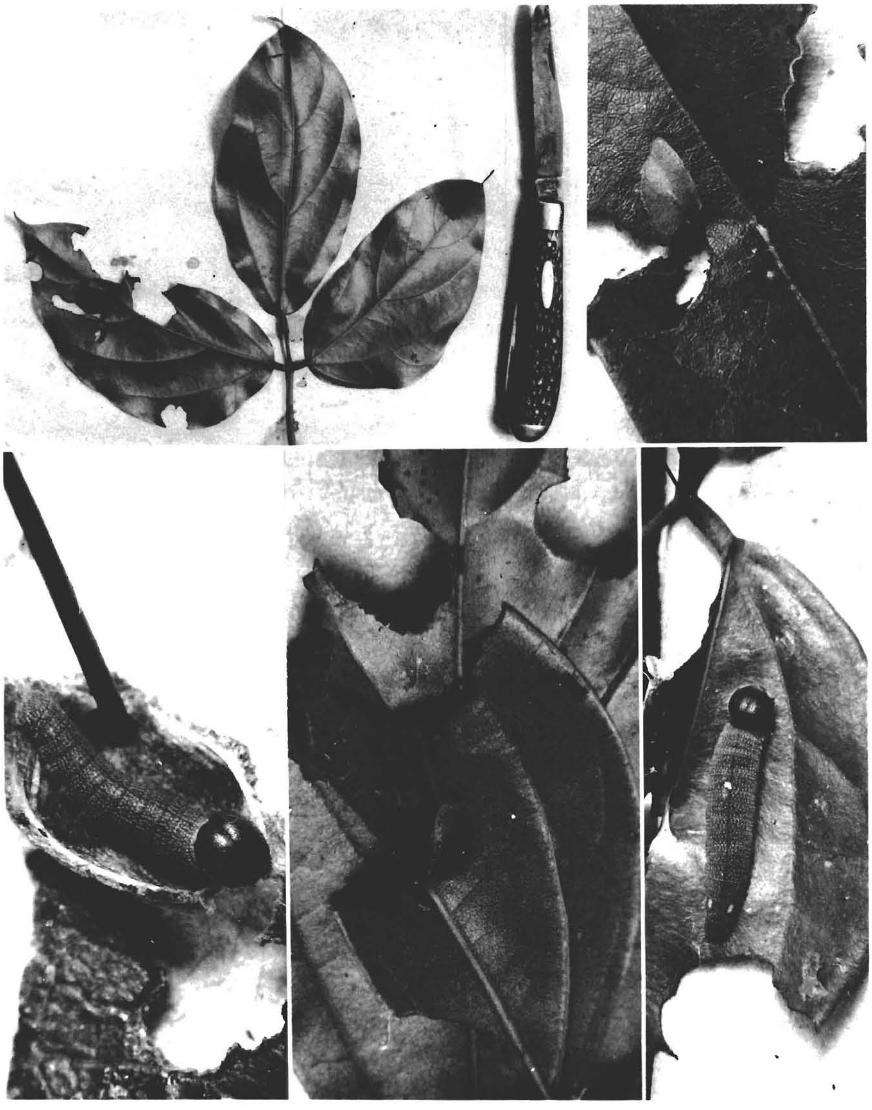

FIG. 2. *Urbanus proteus* natural history. Upper panel, left to right: *Mucuna* leaves showing characteristic feeding pattern of young caterpillar; dorsal view of tent shelter of second-instar caterpillar on the dorsal surface of the leaf. Bottom panel, left to right: third-instar caterpillar perching on silk mat on the "roof" portion of tent shelter; fourth-instar tent shelter from dorsal aspect and with caterpillar hidden from view; fourth-instar caterpillar perched on "roof" portion of tent shelter shown in the previous photograph (match up areas of leaf damaged by larval feeding).

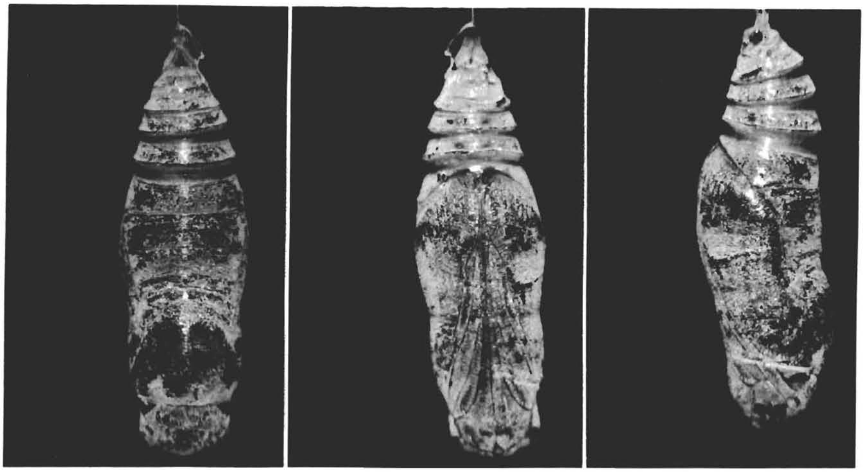

FIG. 3. Dorsal, ventral, and lateral views of pupa of *Urbanus proteus*, respectively.

but with thin border of orange. Later instars fashion tent shelters by tying together two lobes of the tri-lobed *Mucuna* leaf (Fig. 2); always solitary. Entire larval period lasts about 45 days, with transition from third to last (fifth) instar in about 20 days with an increase of 16 mm in body length (from 19 to 35 mm). The 21 mm long × 6 mm wide chestnut brown pupa is generously dusted with a bluish white pubescence (Fig. 3) and is formed with the tent shelter used by the final instar caterpillar. Eclosion takes place in about 16 days. In Costa Rica, caterpillars of *U. proteus* appear to be dusk or nocturnal feeders. It is very likely that this species occurs on a broad range of legumes in Costa Rica as noted elsewhere (e.g., Comstock & Vazquez, 1961, Ann. Inst. Biol. 31:349–448; Howe, op. cit.).

Astraptes fulgerator Natural History

Egg very similar to that of *U. proteus* except 2.0 mm diameter and placed on both meristem and mature food plant leaves. In a large patch of *Erythrina* sp. (Leguminosae) seedlings all less than 0.5 m tall in the cacao grove at La Lola, a fresh appearing female placed one egg each on a total of five seedlings within a two minute period one morning. In each case, the butterfly alighted on the underside of a large meristem leaf and quickly affixed an egg to it (12 March 1983). At La Tigra, one female distributed a total of eight eggs within a 7.0 m tall *Erythrina* tree over several minutes during a morning of intermittent drizzle and sunshine. All eggs were affixed singly to the undersides of mature leaves, one egg per leaf and widely scattered throughout the lower portion of the leafy canopy. During a drizzle spell, the butterfly flew off, only to return about ten minutes later to resume oviposition in this tree. Egg hatching involves devouring only the top portion of the shell, and the caterpillar (about 3 mm long with reddish brown body and large black head capsule) immediately crawls to the edge of the same leaf and constructs a tent shelter in a manner identical to that described earlier for *U. proteus*. The first and second instar larva rests on the underside of the "roof" leaf flap of the shelter; later instars build larger tents as also noted for *U. proteus*. Fifth instar larvae of *A. fulgerator* were found at Ojo de Agua (26 February 1984) feeding on mature leaves of *Calea urticifolia* (Willd.) (Compositae) and a single fifth instar of this species was found on *Trigonia rugosa* Benth. (Trigoniaceae) at Barranca a week later (2 March 1984). In both cases, larvae were concealed inside tent shelters similar to those found on *Mucuna* for an unidentified species of the same genus (see below) and for *U. proteus*. Both food plant shrubs possessed predominantly mature, well-worn, and heavily insect damaged leaves, with little or no meristem leaves evident during this dry season period (January–April) at both localities. Mature caterpillars of *A. fulgerator* were present on both food plants at a time when meristem leaves were either entirely absent (*T. rugosa*) or very scarce (*C. urticifolia*). For *C. urticifolia* there was a mean length ($\bar{x} \pm$ S.D.) of 1.02 ± 0.43 cm for meristem leaves (defined here as soft unfurling leaves within the length range of 0.2–4.0 cm) for a total of 18 leaves measured on three branches on 26 February 1984. On 15 March 1984, $\bar{x} \pm$ S.D. was 2.54 ± 1.05 cm for a total of 36 meristem leaves within the same size range on the same three branches. In captivity *A. fulgerator* fifth instars successfully completed development on the mature, worn leaves of their food plants. When the caterpillar and its woody vine-like food plant shrub were discovered along a foot path within the Barranca forest habitat (Fig. 4), a freshly eclosed adult *A. fulgerator* was netted about 10 m from the spot one hour later.

The fifth instar caterpillar of *A. fulgerator* attains a body length of 48 mm, a maximal body width of 8 mm, and a head capsule width of 6 mm. The reddish brown, markedly bi-lobed head capsule is densely covered with short-to-long white hairs (Fig. 5). The neck "collar" is yellowish orange and the ground color of all body segments is a deep wine-red; each body segment with a thick transverse white band, and the entire body is blanketed with fine white hairs of varying lengths (Fig. 5). The anal plate is dull red as are all legs. During the daytime, the caterpillar remains well concealed in a shelter formed by folding over a portion of leaf and anchoring it with a few silk threads (Fig. 5). The pupa is housed in a tent shelter formed by pulling together two or more adjacent leaves (Fig. 5). The pupa itself is very similar to that of *U. proteus*, but measuring 25 mm long by 9 mm wide; the cuticle is generously covered with a dusting of bluish white pubescence (Fig. 5). Eclosion takes place in about 19 days.

Unidentified *Astraptes* Natural History

The fifth instar caterpillar stage of an unidentified *Astraptes* was found concealed in a tent shelter on a *Mucuna* vine at Bajo La Hondura (26 December 1972) (Fig. 6). The caterpillar was 35 mm long when discovered and grew to 50 mm in length by 18 January 1973, at which time a massive number of larvae of an endoparasite emerged from it and formed a mass of cocoons on the cuticle (Fig. 6). The caterpillar is dark brown with conspicuous lateral blotches of pale green; the anal plate is dull red and the head capsule a glossy dark brown. The head capsule is covered with short reddish hairs. A second caterpillar found at this site was reared to the pupa stage. About two days prior to pupation, it became an active, orange colored prepupa, eventually pupating within its tent shelter. The 25 mm long by 8 mm thick pupa similar to those previously described. The parasitized caterpillar yielded a total of 100 *Apanteles* sp. wasps (Hymenoptera: Braconidae: Microgasterinae), a group known only to be endoparasites of Lepidoptera caterpillars (P. M. Marsh, pers. comm.).

Astraptes fulgerator has been reported as feeding on various Leguminosae (e.g., Comstock & Vazquez, op. cit.; Howe, op. cit.) and other species of the genus also on legumes (Kendall, op. cit.). The discovery in Costa Rica of this skipper exploiting both Compositae and Trigoniaceae as larval food plants is new to science. Kendall (op. cit.) lists some 11 plant families as being reliable larval food plant records for Hesperiidae in Mexico, but that list does not include Compositae or Trigoniaceae. One plant family that does turn up in hesperiid larval food plant records in the American tropics and subtropics is Malpighiaceae, a group found along with Trigoniaceae in the order Polygalales of the subclass Rosidae (Cronquist, 1981, An integrated system of classification of flowering plants, Columbia, New York, 1262 pp.). Furthermore, the Leguminosae, a common hesperiid larval food plant family and utilized by both *Urbanus* and *Astraptes*, is also within the Rosidae, but in a different order, the Fabales (Cronquist, op. cit.). Howe (op. cit.) summarizes the wide geographical distribution of *A. fulgerator* and the wide variability in the color pattern of the caterpillar stage. It would not be surprising to discover a polyphagous habit in such a species, and this note confirms this pattern for *A. fulgerator* in Costa Rica. While both *Urbanus* and *Astraptes* exploit legumes such as *Mucuna* vines in Costa Rica, the relatively aposematic appearance of *Astraptes* caterpillars compared with the subdued or cryptic-like colors of *Urbanus* caterpillars suggests a divergence in larval

FIG. 4. Habitat and larval food plant of *Astraptes fulgerator* at Barranca. Top: disturbed primary-secondary forest where the larval food plant, *Trigonia rugosa* (Trigoniaceae) was found. Bottom, left and right: habitat area where freshly-eclosed adult *A. fulgerator* netted; *T. rugosa* showing insect-damaged mature leaves (machete for scale).

FIG. 5. *Astraptes fulgerator* natural history. Above panel, left to right: fifth-instar caterpillar, lateral view; tent shelter of fifth-instar caterpillar on *Trigonia rugosa* food plant. Bottom, left to right: tent shelter containing pupa; ventral aspect of pupa showing dusting of pubescence.

defense against predators that possess color perception abilities. While the seeds of some *Mucuna* species possess toxic secondary compounds demonstrated to thwart predation by vertebrates (e.g., Janzen, 1969, Evolution 23:1–27), far less is known about the existence of poisonous compounds within the leaves of these vines. Other herbivores routinely associated with some *Mucuna* species in Costa Rica, such as *Morpho peleides* Kollar

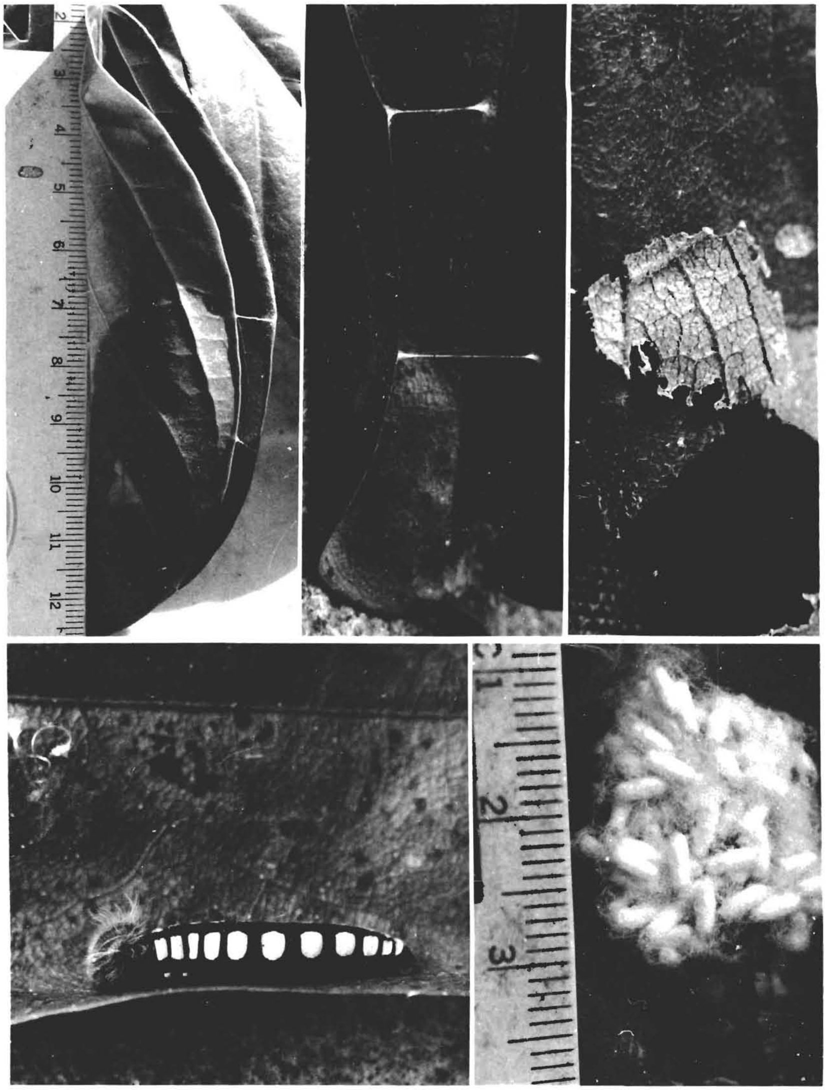

FIG. 6. Unidentified *Astraptes* species natural history. Above panel, left to right: tent shelter of fifth-instar caterpillar on *Mucuna* leaf and showing silken ties; close-up view of silken threads responsible for holding opposite sides of leaf together; tent shelter of an early instar at edge of leaf. Bottom panel, left to right: fifth-instar caterpillar, lateral view; mass of *Apanteles* cocoons on surface cuticle of fifth-instar caterpillar.

(Morphidae), have brightly colored early instar caterpillar stages and adults with iridescent blue wings (e.g., Young & Muyshondt, 1973, Carib. J. Sci. 13:1–49). In some lepidopterans associated as herbivores with plants possessing known toxic properties, some species are able to sequester the toxic compounds, while others, feeding on the same plants, are not able to do so (e.g., Rosenthal & Janzen, eds., 1979, Herbivores: Their interaction with secondary plant metabolites, Academic Press, New York and London, 717 pp.). Thus, the possibility exists that *Astraptes*, with brightly colored caterpillars and adults with iridescent blue wings, have evolved the ability to sequester presumed toxins in the leaves of legume food plants such as *Mucuna*, while *Urbanus* has not evolved such a trait. Further support for a presumed toxicity associated with *Astraptes* is afforded by the *Calea urticifolia* larval food plant record reported here: this plant is known to be extremely toxic owing to high concentrations of sesquiterpenes (L. Poveda, pers. comm.). To the best of my knowledge, *Urbanus* does not feed on Compositae or Trigoniaceae.

The discovery of mature caterpillars of *Astraptes* at the height of the tropical dry season at two localities indicates that these insects are able to exploit mature leaves at such times of the year when meristems are lacking or scarce. The cohort of adult skippers eclosing in the latter half of the dry season might "anticipate" a soon-to-be available supply of fresh meristems on which to place their eggs in the sense of *Phoebis* exhibiting such behavior on its *Cassia* food plant at this time (Young, in press). My data suggests that *Astraptes* will deposit eggs on both mature leaves and meristem leaves. To what extent, if any, does *A. fulgerator* exhibit a facultative seasonal switch in food plant families in Costa Rica awaits further field study. To what extent does *Mucuna* and other legume food plants, fully leafed-out in the rainy season, become inaccessible as larval food sources during the tropical dry season and inducing a switch to alternate food plant groups, remains to be studied. Food plant quality, and temporal changes in it, is a major determinant of food plant choice in some herbivorous insects (e.g., Marian & Pandian, 1980, Entomon 5:257–264; Rausher, 1981, Ecol. Monogr. 51:1–20; Hill, 1982, Zool. Jahrb. Abt. Syst. Okol. Geogr. Tiere 109:24–32; Lawson et al., 1982, Entomol. Exp. Appl. 32: 242–248; Messina, 1982, Oecologia 55:342–354; Miles et al., 1982, Aust. J. Zool. 30:347–355; Wint, 1983, J. Anim. Ecol. 52:438–450). Some skippers exhibit seasonal shifts in the use of their larval food plants (e.g., Nakasuji, 1982, Appl. Entomol. Zool. 17:146–148). A polyphagous insect such as *A. fulgerator* in Costa Rica may possess the complement of mixed-function oxidases within the guts of caterpillars to permit the expression of a generalist feeding behavior involving different food plant families exhibiting both qualitative and quantitative differences in the profiles of toxic compounds functioning to deter herbivorous attack (e.g., Ahmad, 1983, Ecology 64:235–243). Finally, within a relatively small region of the American tropics, a polyphagous species such as *A. fulgerator* may have undergone an evolutionary divergence in the use of different larval food plant families. Sometimes such geographical divergence reaches the point at which caterpillars from different populations cannot survive on food plants other than those found in their own habitats (e.g., Kaufmann, 1983, Proc. Entomol. Soc. Wash. 85:321–326). I was unable to detect any noticeable difference in coloration between the caterpillars of *A. fulgerator* from Ojo de Agua and Barranca, and the sample was very small. *Astraptes* caterpillars may use tent shelters on their food plants as a means of hiding from parasitoids such as *Apanteles* and Tachinidae, but such behavior does not always ensure survival as noted in this paper.

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