

ANTS, BIRDS, AND SKIPPERS

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ABSTRACT.— A large number of skipper species (Lepidoptera: Hesperidae) were found associated with army ant swarms in Brazil. These butterflies aggregate to feed on the droppings of birds attracted to the insects flushed by advancing swarms. In contrast to the female-dominated use of bird droppings by ithomiine butterflies, skipper use was almost exclusively by males.

KEY WORDS: Argentina, army ants, Aves, behavior, birds, Brazil, droppings, Formicidae, Hesperidae, Hymenoptera, Mexico, Neotropical, nutrients, skippers.

Western Brazil harbors one of the highest diversities of butterflies known (Brown, 1984; Emmel, 1989; Emmel and Austin, 1990). We have cooperated in studies of the butterfly fauna at Fazenda Rancho Grande in the vicinity of Cacaullandia, Rondônia, Brazil, since March 1989 (see Emmel and Austin, 1990), an area characterized by typical lowland tropical rainforest vegetation. This fauna is now known to exceed 1200 species (Austin and Emmel, unpubl. data).

During November 1989, the senior authors were intrigued by a report on the apparent occurrence of mixed-species aggregations of large forest skippers (Hesperidae). We initially thought that this behavior might be indicative of the formation of leks analogous to that found among certain Ithomiinae (Nymphalidae) (DeVries, 1987). In November 1990, Brock encountered an aggregation of skippers and noted that observations were impeded because it was among a swarm of ants. It was not until later that the potential significance of the latter observation was realized. We herein record our observations of species composition and behavior of skipper aggregations at Fazenda Rancho Grande and speculate on their formation and significance.

ARMY ANTS

Army ant (Formicidae: Ecitoninae) swarms are a familiar feature in the lowlands of the Neotropics. Army ant movements and other activities have been of interest to biologists since this region was first investigated (Bates, 1863) and remain so to the present. Ants grouped under this designation are generally defined as carnivorous species with no or vestigial compound eyes which forage in groups and move their nest site on a regular basis (Wilson, 1958; Rettenmeyer, 1963; Schneirla, 1971). Of the approximately 150 species in the New World, two species of the tribe Ecitonini form large aboveground swarms and occur from Mexico to Argentina.

The first of these with truly spectacular raids, *Eciton burchelli* (Westwood), has been studied extensively (Rettenmeyer, 1963;

Schneirla, 1956, 1957, 1971) and its behavior and ecology have been outlined by Willis (1967a), Rettenmeyer (1983), and Hölldobler and Wilson (1990, see also color photographs of these ants in Willis, 1972a). The following summary is based on these papers and our observations in Rondônia. This rather large species (3-10mm) with polymorphic workers occurs in huge colonies of up to several hundred thousand individuals. They live in a temporary aboveground nest called a bivouac formed by clusters of clinging ants beneath a log or other fallen vegetation. The bivouac may be moved nightly or remain stationary for several days, depending on the stage of the reproductive cycle.

Foraging is usually done during daylight hours, commences in the morning, and often lasts throughout the day. During some periods of the reproductive cycle, foraging may start later in the day or not occur at all. Foraging is initiated when huge numbers of ants move out of the bivouac; these concentrate in one direction and form a swarming front that may be as much as 15m wide but usually narrower. The swarm moves across the forest floor, flushing prey as it advances. Many arthropods (plus occasional terrestrial vertebrates) flee as they are approached by the ant swarm (e.g., Otis *et al.*, 1986). The front remains connected to the bivouac by one or more columns of ants moving in both directions either returning food to the nest or moving to the front. Behind the front, the main column breaks into a fan shape of numerous, often interconnected, smaller columns.

Swarms of *E. burchelli* are regularly attended by an array of insects including wasps, beetles, and, especially, flies (Akre and Rettenmeyer, 1966; Rettenmeyer, 1961, 1983, see table in Hölldobler and Wilson, 1990) and by birds (Johnson, 1954; Willis, 1966; Willis and Oniki, 1978). These largely prey upon or parasitize arthropods fleeing the advancing swarm. Often the observer is aware of the sound of flies or the presence of birds before he is cognizant of the proximity of ants.

The second species that forms large aboveground swarms is *Labidus praedator* (F. Smith). This species was studied by Borgmeier (1955) and Rettenmeyer (1963) and its behavior and ecology summarized by Willis (1967a). *Labidus* is a small (2-7 mm) generally black (versus the two-toned red-brown of *E. burchelli*) ant which lives in concealed bivouacs. It forms large

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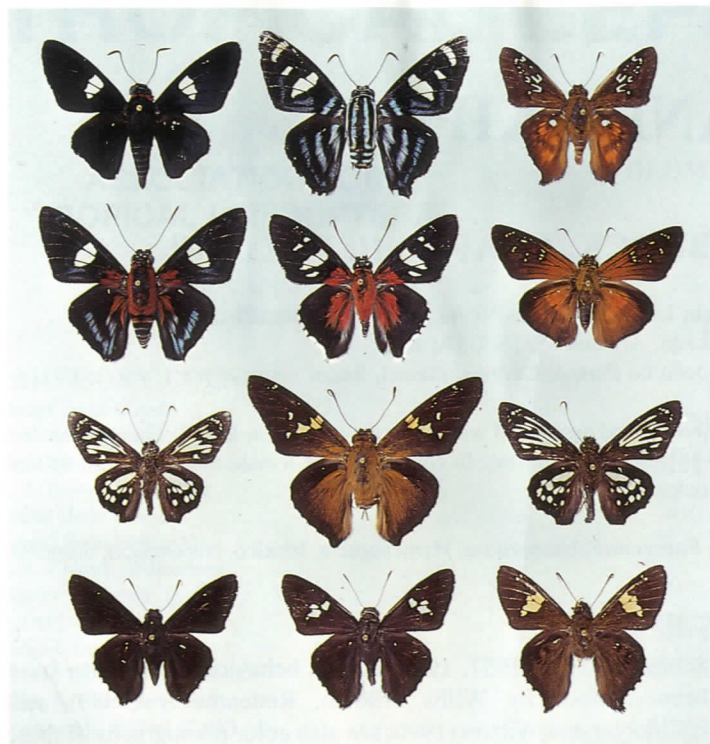


Fig. 1. Some pyrrhopygine and pyrgine skippers associated with army ants in Rondônia, Brazil. Left to right, top row - *Pyrrhopyge rubricollis*, *Elbella patrobas*, *Heronia labriaris*; second row - *Tarsoctenus praecia*, *Tarsoctenus corytus*, *Augiades criniscus*; third row - *Phanus* species, *Epargyreus clavicornis*, *Phanus obscurior*; bottom row *Chrysoplectrum otriades*, *Chrysoplectrum perniciosus*, *Cephise* species.

swarms which may reach 4m or more across. These swarms move irregularly across the forest floor, first moving in one direction and then in another, at times covering the same piece of ground more than once. The raids of *Labidus* apparently do not last as long as those of *E. burchelli* but this impression may be the result of the difficulty in following a swarm along its unpredictable course. This species also moves more beneath the leaf litter and into cracks and tunnels in the ground than does *E. burchelli*, making it even more difficult to observe.

As with *Eciton*, swarms of *Labidus* flush arthropods as they advance. We have found that they are similarly attended by flies, wasps, and other insects. Birds also follow these ants but less regularly than *Eciton* (Willis, 1966).

ANT ASSOCIATED BIRDS

Several species of birds forage at swarms of army ants, particularly those of *Eciton burchelli* and *Labidus praedator*. These birds were noted by Johnson (1954), extensively studied by Willis (1960, 1966, 1967a, 1967b, 1968, 1969, 1972a, 1972b, 1979, 1982a, 1982b), and reviewed by Willis and Oniki (1978). The following is summarized from those investigations.

Ant associated birds occur in varying numbers, frequencies, and fidelities with swarming ants. Some of these are specialists, including certain species of woodcreepers (Dendrocolaptidae) and antbirds (Formicariidae), which obtain the majority of their food from arthropods fleeing before an ant swarm, follow individual swarms for days at a time, and are rarely encountered away from these situations. Their reproductive activities and territorial behaviors may be modified to a greater or lesser extent by the

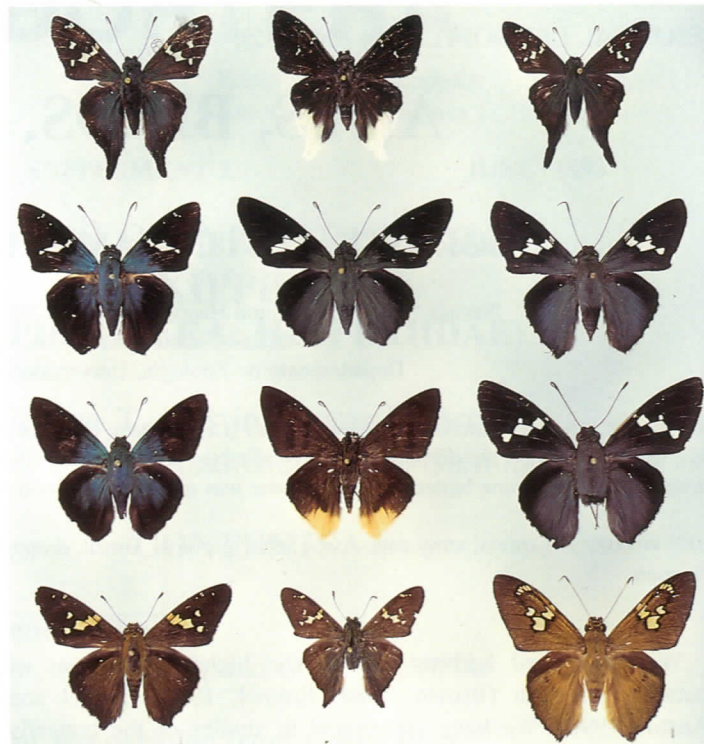


Fig. 2. Some pyrgine skippers associated with army ants in Rondônia, Brazil. Left to right, top row - *Urbanus prouta*, *Urbanus reductus*, *Urbanus acawoios*; second row - *Astraptus fulgerator*, *Astraptus apastus*, *Astraptus janeira*; third row - *Astraptus alector*, *Astraptus anaphus*, *Narcosius colossus*; bottom row - *Aguna asander*, *Aguna hypozeonius*, *Nascus solon*.

activities of army ants. Other species forage at ant swarms less frequently or only casually. When more than one specialist species is feeding at a swarm, the foraging space is partitioned (see diagram in Willis, 1972a) and the prey taken varies concomitantly (Chapman and Rosenberg, 1991). Dominant (generally larger) bird species occupy an area immediately above and just in front of the advancing swarm, where they perch only a few centimeters above the ants and sally forth to capture escaping insects. Subdominant bird species occupy an area above and around the dominants but still near the main portion of the advancing swarm. Subordinate taxa forage peripherally in the region behind the advancing front and along the columns extending to the bivouac.

Ant associated birds may locate ant swarms by attraction to the calls or presence of other ant associated birds, by the movement of the ants themselves and their associated flies, or by large numbers of flushing prey. Individual birds may follow ant swarms for many days by relocating them at first light. If a column is detected first, a bird may fly along this trail until the swarming front is located, backtracking when necessary if the encountered column leads to a minor front or to the bivouac.

These resident birds forage most often at swarms of *Eciton burchelli* since they occur in larger colonies, are more regular in their movements and thus are easier to follow throughout the day and from day to day, and they flush larger prey on the average. The aboveground activities of *Labidus praedator* tend to be more seasonal and often do not persist for more than a few hours at a time. In at least some Neotropical localities, a number of migrant bird species also forage at ant swarms, mainly at those of *Labidus*, and are subordinate to resident species at swarms of either ant species.



Fig. 3. Some pyrgine and hesperiine skippers associated with army ants in Rondônia, Brazil. Left to right, top row - *Porphyrogenes suva*, *Ablepsis amazonensis*, *Marela tamyroides*; second row - *Telemiades epicalus*, *Aethilla echina*, *Grais stigmaticus*; third row - *Carystoides orbius*, *Panoquina fusina*, *Saliana salius*; bottom row - *Neoxeniades seron*, *Aides duma*, *Aides aegita*.

Several species of known ant associated birds (e.g., see Meyer de Schauensee and Phelps, 1978; Willis, 1960, 1967b, 1968, 1969, 1972b, 1982a) have been recorded at Fazenda Rancho Grande (from list prepared by R. S. Ridgely). These include woodcreepers (*Dendrocincla fuliginosa*, *Hylexetastes perrotii*, *Dendrocolaptes concolor*) and antbirds (*Rhegmatorhina hoffmannsi*, *Phlegopsis nigromaculata*, *Formicarius analis*). We have seen birds of both families associated with the ant swarms that we studied (two swarms were located by following bird calls) but we have not attempted to identify or study them.

ANT SKIPPERS

Methods

As indicated above, we did not realize the significance of the cooccurrence of army ants and skippers until after our return from Rondônia in late 1990. We developed the hypothesis that skippers were attracted to army ants by the potential concentration of a nutrient source (bird droppings) left by ant associated birds. We finally were able to test this in November and early December 1991. At that time, the junior author confirmed the association of ants, birds, and skippers through his extensive experience in tropical America. Our first contacts with ant swarms were late in the day but we noted numerous large skippers in attendance. As we had postulated, these were obviously investigating white objects and stopped to feed when a bird dropping was encountered.

These observations prompted us to make a concerted effort to locate swarming ants and to initiate preliminary studies of species diversity and behavior of skippers at army ant swarms. We

contemplated using various white objects as lures to augment already present bird droppings and finally settled on the use of pieces of saliva-moistened toilet paper (as suggested by Mielke) placed on low-growing leaves among and adjacent to the foraging ants. Saliva not only aided in affixing the paper to leaves, but it apparently also provided moisture or some nutrient for the butterflies (and other insects), and thus facilitated observation and capture. As a control, saliva-moistened paper was placed similarly in the same habitat away from swarming ants.

Indices of abundance are expressed as number taken per ten collecting hours in the Cacaulandia area by the senior author. This represents 766 general collecting hours on 109 days (March, October-November 1989; October-December 1990; March-April, November-December 1991). While these collections are biased to some degree since all butterfly species were of interest, special attention was paid to hesperiids and especially to species not previously encountered. In addition, in November-December 1991, 33.5 hours on six days were spent at swarms of *E. burchelli*, 11.5 hours on four days with swarms of *L. praedator*, and 12 hours on two days collecting at toilet paper lures away from ant swarms. For comparative purposes, all data presented are those of the senior author. Also data are given on the occurrence of ant associated skippers in traps baited with putrid fish (and sometimes bananas), again during November-December 1991. This represents 347 trap days of effort. Butterfly size is length of the forewing from base to apex in mm. This was measured for one specimen of each species and the mean size is presented for each subfamily and the entire known skipper fauna at our study area.

Results

Each of the six swarms of *E. burchelli* and four swarms of *L. praedator* encountered was attended by hesperiids (Figs. 1-11). Skippers were seen in all areas where ants were active including at the bivouac, along the columns, and at the swarm front. The butterflies usually flew less than 0.5 m above the ants often patrolling the length of the ant columns between the swarm and bivouac. All species invariably paused to investigate white objects encountered on the ground or on low leaves above the ground. If such was a bird dropping, they would usually stop to feed, often returning time and again to the same dropping even if this was continually overrun with ants. Similar behavior was noted at our paper lures. On occasion, the lure fell off the leaf as the butterfly alighted. Once, a *Tarsoctenus* rode the paper to the ground; individuals of other species returned immediately.

The numbers of skipper species and individuals associated with swarms of army ants are impressive (Table 1, 2) with an average of 27 species (38 at swarms observed for four hours or more) and 50 individuals (73 at swarms observed for four hours or more) taken per swarm. The numbers varied widely; as many as 53 species were seen and 111 specimens were taken during 7.5 hours at a swarm of *E. burchelli* on 5 December. A total of 110 species was seen at the swarms we studied. Of these, 94 were recorded at *Eciton* swarms and 56 at *Labidus* swarms. Too few data exist to meaningfully compare numbers, frequencies, and species composition at swarms of *Eciton* and *Labidus*.

The species associated with ants may be divided into three

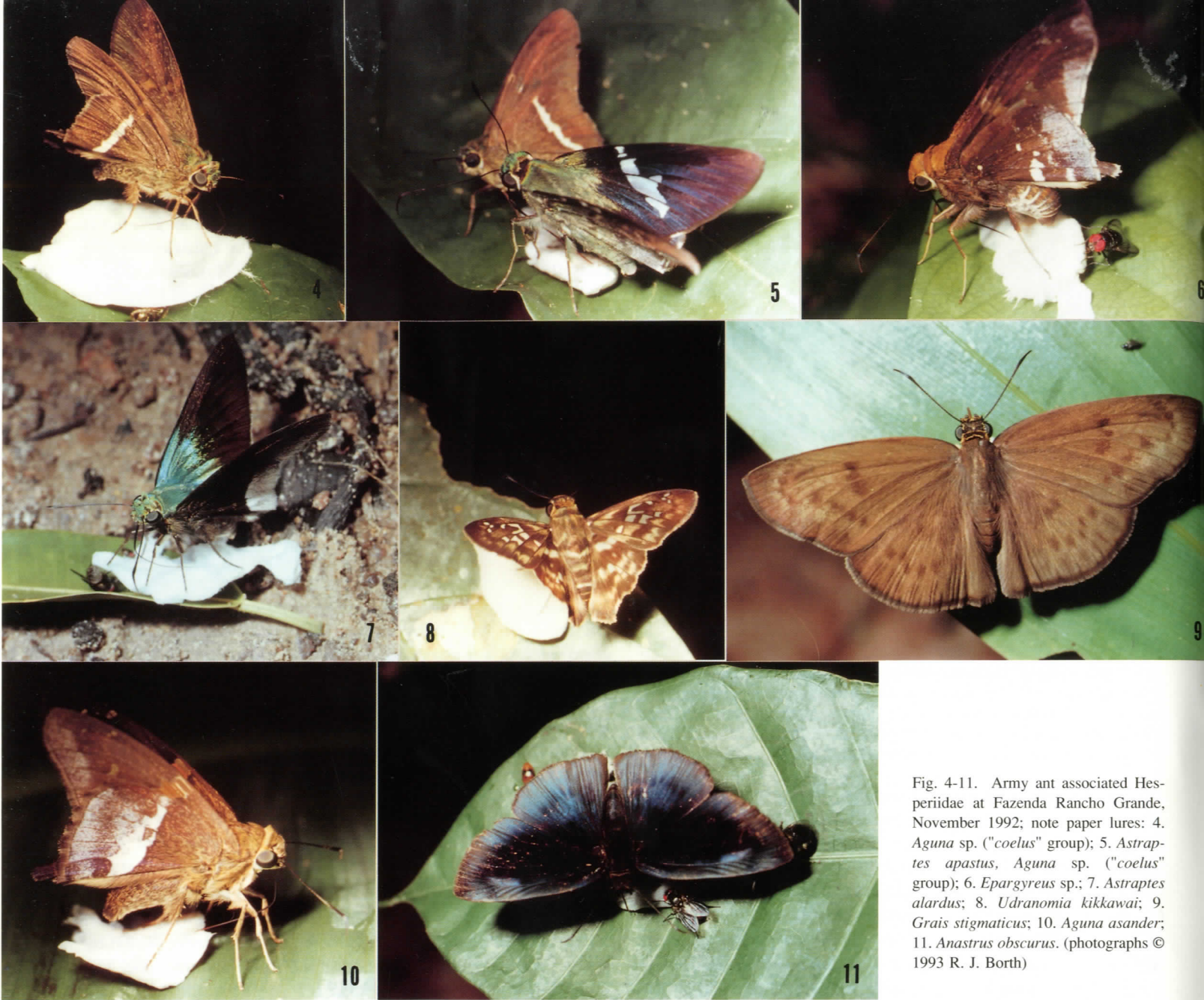


Fig. 4-11. Army ant associated Hesperidae at Fazenda Rancho Grande, November 1992; note paper lures: 4. *Aguna* sp. ("coelus" group); 5. *Astraptes apastus*, *Aguna* sp. ("coelus" group); 6. *Epargyreus* sp.; 7. *Astraptes alardus*; 8. *Udranomia kikkawai*; 9. *Grais stigmaticus*; 10. *Aguna asander*; 11. *Anastrus obscurus*. (photographs © 1993 R. J. Borth)

rough groups on the basis of their frequency at ant swarms and their abundance at and away from swarms (Table 3). The first are taxa relatively frequent and common at swarms and are taken in low numbers away from swarms. These are all pyrgines and include *Phanus*, *Augiades*, *Epargyreus* (except *E. exadeus*), several *Aguna*, *Typhedanus*, three *Urbanus*, several *Astraptes*, *Marela*, *Aethilla*, and *Grais*. The majority of these were also taken in traps and at paper lures away from ants. The second group is of species taken in approximately equal numbers with and without ants. These include *Hyalothyris*, *Autochton*, and several others; are thought to be casually associated with ants when they are in their vicinity; and are rarely taken in traps or at paper lures away from ants. The third group are species infrequent and generally in low numbers at ant swarms and are also rare away from swarms (over half have not been taken in 766 hours of general collecting). More than 75% these species have not been taken in traps or at paper lures.

The taxonomic composition of skippers associated with army ants indicates that pyrgines use the associated resource propor-

tionally more than either pyrrophygines or hesperiines (Table 4). Over 32% of the pyrgine species known from the Rancho Grande area have been recorded at ant swarms compared with less than 20% of the other two subfamilies. Nearly three-quarters of the skipper species associated with ant swarms and nearly 90% of the individuals collected there are pyrgines. Ant skippers also average larger in size than those species not associated with ants (Table 4).

There were some apparent differences in the species present at ant swarms at different times of the day. The most obvious was the appearance of crepuscular taxa (*Nascus*, *Dyscophellus*, *Carystoides*) late in the day at the time when many of the species seen earlier had disappeared. There also appeared to be definite activity patterns for some of the other species but this needs to be documented. The appearance of new individuals at the ant swarm seemed to occur throughout the day. At times, we would see practically no skipper activity in the vicinity of the ants and a short while later there would be much activity. Some observed individuals disappeared entirely from the vicinity of the swarm.

TABLE 1. Hesperidiidae associated with army ant swarms in Rondônia, Brazil (nomenclature in Appendix I). Data given are number of males/females separately for *Eciton* (33.5 hours) and *Labidus* (11.5 hours) swarms, frequency combined (N = 10 swarms), and average number per ten hours combined. Comparative data are given for these same species at paper lures (12 hours), during general collecting (766 hours), their occurrence in bait traps, and forewing length of males.

Species	ANT SWARMS				PAPER LURES		GENERAL		presence in traps	forewing length (mm)
	<i>Eciton</i> m/f	<i>Labidus</i> m/f	freq.	no./ 10 hrs	m/f	no./ 10 hrs	m/f	no./ 10 hrs		
<i>P. rubricollis</i>	1/0	-	10	0.22	-	-	-	-	-	25.6
<i>E. patrobas</i>	1/0	-	10	0.22	-	-	-	-	-	28.1
<i>T. corytus</i>	-	2/0	20	0.44	-	-	-	-	-	25.8
<i>T. praecia</i>	3/0	-	10	0.67	-	-	-	-	-	27.1
<i>P. vitreus</i>	24/1	15/1	80	9.11	3/0	2.50	4/2	0.08	x	20.7
<i>Phanus</i> sp.	14/1	5/0	80	4.44	3/0	2.50	6/1	0.09	x	20.2
<i>P. obscurior</i>	6/0	2/0	50	1.78	-	-	2/2	0.05	x	22.3
<i>P. marshallii</i>	6/0	2/0	50	1.78	2/0	1.67	6/5	0.14	-	22.2
<i>U. kikkawai</i>	-	1/0	10	0.22	-	-	-	-	-	14.6
<i>A. criniscus</i>	13/0	-	40	2.89	1/0	0.83	1/0	0.01	x	23.1
<i>H. infernalis</i>	-	1/0	10	0.22	-	-	9/4	0.17	-	20.7
<i>H. neleus</i>	1/0	-	10	0.22	1/0	0.83	14/11	0.33	-	21.2
<i>E. clavicornis</i>	13/0	5/0	90	4.00	5/0	4.17	6/0	0.08	x	29.5
<i>E. socus</i>	8/0	1/0	60	2.00	1/0	0.83	-	-	x	28.2
<i>E. exadeus</i>	2/0	-	20	0.44	1/0	0.83	-	-	x	30.0
<i>A. asander</i>	6/1	1/0	50	1.78	-	-	3/2	0.07	x	24.1
<i>A. aurunce</i>	1/0	1/0	20	0.67	-	-	0/1	0.01	-	25.9
<i>A. coelus</i>	3/0	1/0	30	0.89	1/0	0.83	3/2	0.07	-	20.5
<i>A. hypozonius</i>	12/0	4/0	70	3.56	2/0	1.67	23/3	0.34	x	20.0
<i>Aguna</i> sp.	1/0	4/0	30	1.11	2/0	1.67	1/0	0.01	x	21.0
<i>A. metophis</i>	6/0	3/0	70	2.00	-	-	3/1	0.05	-	19.7
<i>T. optica</i>	5/0	2/0	40	1.56	-	-	23/4	0.35	x	19.1
<i>P. auginus</i>	1/0	-	10	0.22	-	-	1/0	0.01	-	16.5
<i>H. labriaris</i>	2/0	-	10	0.44	-	-	-	-	x	21.0
<i>C. otriades</i>	3/0	1/0	30	0.89	-	-	-	-	-	20.8
<i>C. perniciosus</i>	4/0	-	30	0.89	-	-	-	-	-	21.0
<i>C. pervivax</i>	-	1/0	10	0.22	-	-	1/0	0.01	-	20.2
<i>U. prona</i>	6/0	3/0	50	2.00	3/0	2.50	15/2	0.22	x	20.4
<i>U. esta</i>	1/0	1/0	20	0.44	1/0	0.83	6/1	0.09	-	18.5
<i>U. belli</i>	1/0	4/0	30	1.11	1/0	0.83	1/3	0.05	-	22.8
<i>U. esmeraldus</i>	1/0	2/0	20	0.67	-	-	-	-	-	19.5
<i>U. acawoios</i>	1/0	-	10	0.22	-	-	-	-	x	21.0
<i>U. teleus</i>	1/0	-	10	0.22	-	-	26/6	0.42	-	22.3
<i>U. carmelita</i>	2/0	3/0	40	1.11	1/0	0.83	1/3	0.05	-	21.0
<i>U. chalco</i>	1/0	-	10	0.22	-	-	3/1	0.05	-	22.6
<i>U. reductus</i>	4/0	-	30	0.89	2/0	1.67	3/0	0.04	-	22.2
<i>U. doryssus</i>	11/0	4/0	60	3.33	4/1	4.17	27/8	0.46	x	21.0
<i>A. fulgurator</i>	33/0	22/0	90	12.22	3/0	2.50	19/3	0.29	x	26.4
<i>A. halesius</i>	-	1/0	10	0.22	-	-	-	-	-	22.3
<i>A. apastus</i>	16/0	1/0	70	3.78	-	-	2/1	0.04	x	29.9
<i>A. enotrus</i>	2/0	-	20	0.44	-	-	4/1	0.07	x	25.0
<i>A. janeira</i>	5/0	3/0	30	1.78	-	-	3/0	0.04	x	23.8
<i>A. alardus</i>	8/1	5/0	60	3.11	3/0	2.50	7/1	0.10	x	27.1
<i>A. alector</i>	4/1	7/0	70	2.67	2/0	1.67	1/0	0.01	x	23.4
<i>A. latimargo</i>	2/0	-	20	0.44	-	-	-	-	x	24.8
<i>A. anaphus</i>	4/1	3/0	50	1.78	-	-	6/0	0.08	x	26.0
<i>N. parisi</i>	1/0	1/0	20	0.44	-	-	1/0	0.01	-	27.5
<i>N. colossus</i>	6/0	-	40	1.33	-	-	-	-	-	32.1
<i>N. nazaraeus</i>	3/0	1/0	30	0.89	-	-	-	-	-	33.8
<i>Narcosius</i> sp.	1/0	2/0	20	0.67	-	-	-	-	-	30.0
<i>C. zeutus</i>	1/0	-	10	0.22	-	-	1/0	0.01	-	26.2

TABLE 1 (cont.)

<i>Cephise</i> sp.	1/0	-	10	0.22	-	-	-	-	-	22.0
<i>A. longipennis</i>	-	2/0	20	0.44	-	-	26/13	0.51	-	18.2
<i>A. zarex</i>	1/1	-	20	0.44	-	-	21/13	0.44	-	16.4
<i>A. neis</i>	1/1	-	20	0.44	-	-	19/5	0.31	-	16.2
<i>D. euribates</i>	1/0	-	20	0.22	1/0	0.83	1/0	0.01	x	28.4
<i>N. phocus</i>	2/0	-	20	0.44	-	-	-	-	x	26.7
<i>N. solon</i>	1/0	-	10	0.22	-	-	-	-	x	29.3
<i>P. vulpecula</i>	1/0	-	10	0.22	-	-	-	-	-	23.9
<i>P. spanda</i>	1/0	-	10	0.22	-	-	-	-	-	19.0
<i>P. suva</i>	1/0	-	10	0.22	-	-	-	-	-	26.7
<i>Porphyrogenes</i> sp.	1/0	-	10	0.22	-	-	-	-	-	22.9
<i>A. amazonensis</i>	1/0	-	10	0.22	-	-	-	-	-	22.6
<i>S. clonius</i>	1/0	-	10	0.22	-	-	10/0	0.13	x	21.1
<i>M. tamyroides</i>	8/0	1/0	40	2.00	2/0	1.67	0/1	0.01	x	21.0
<i>T. delalande</i>	1/1	-	20	0.44	-	-	19/22	0.54	x	21.8
<i>T. squanda</i>	-	1/0	10	0.22	-	-	-	-	-	19.6
<i>T. nicomedes</i>	4/0	-	20	0.89	-	-	1/0	0.01	x	16.2
<i>T. epicalus</i>	2/0	1/0	20	0.67	3/0	2.50	1/0	0.01	-	18.6
<i>T. penidas</i>	1/0	-	10	0.22	-	-	-	-	x	20.0
<i>P. corbulo</i>	1/0	-	10	0.22	-	-	1/0	0.01	-	18.1
<i>S. artemides</i>	2/0	-	10	0.44	-	-	-	-	-	15.6
<i>Q. fanda</i>	1/0	-	10	0.22	-	-	-	-	-	13.0
<i>P. jovianus</i>	1/0	-	10	0.22	-	-	13/2	0.20	-	18.8
<i>M. pilumnus</i>	1/0	-	10	0.22	-	-	1/1	0.03	-	14.7
<i>C. lucaria</i>	4/0	-	20	0.89	-	-	-	-	-	13.0
<i>A. echina</i>	9/0	2/0	40	2.44	2/0	1.67	13/1	0.18	x	25.6
<i>A. busirus</i>	2/2	-	30	0.89	1/0	0.83	21/5	0.34	x	27.6
<i>G. stigmaticus</i>	3/0	3/0	40	1.33	-	-	9/4	0.17	x	24.4
<i>A. obscurus</i>	1/0	-	10	0.22	-	-	1/2	0.04	-	21.0
<i>C. impressus</i>	2/0	-	10	0.44	-	-	4/0	0.05	-	16.0
<i>C. enega</i>	1/0	-	10	0.22	-	-	-	-	-	16.2
<i>S. silius</i>	2/0	-	20	0.44	-	-	59/12	0.93	-	13.1
<i>V. caeruleans</i>	-	1/0	10	0.22	-	-	1/0	0.01	-	14.4
<i>P. proximus</i>	1/0	-	10	0.22	-	-	27/13	0.52	-	17.3
<i>C. nero</i>	-	1/0	10	0.22	-	-	23/3	0.34	-	14.4
<i>V. phyllus</i>	-	1/0	10	0.22	-	-	1/0	0.01	-	17.1
<i>N. orius</i>	-	1/0	10	0.22	-	-	-	-	-	20.2
<i>V. verticalis</i>	1/0	1/0	20	0.44	-	-	-	-	-	15.8
<i>D. dubius</i>	-	1/0	10	0.22	1/0	0.83	0/1	0.01	-	18.0
<i>T. variegata</i>	1/0	-	10	0.22	-	-	0/1	0.01	-	23.8
<i>D. clavus</i>	1/0	-	10	0.22	-	-	2/0	0.03	-	21.6
<i>C. basoches</i>	-	1/0	10	0.22	-	-	-	-	-	23.0
<i>C. noseda</i>	1/0	-	10	0.22	-	-	3/0	0.04	-	21.9
<i>C. lebbaeus</i>	-	1/0	10	0.22	-	-	-	-	-	21.2
<i>C. orbis</i>	3/0	-	10	0.67	-	-	-	-	-	19.6
<i>C. cathaea</i>	1/0	1/0	20	0.44	-	-	0/1	0.01	-	24.1
<i>P. deceptus</i>	1/0	2/0	30	0.67	1/0	0.83	1/0	0.01	-	25.2
<i>O. cynisca</i>	1/0	-	10	0.22	-	-	1/0	0.01	-	24.9
<i>D. lucifer</i>	-	1/0	10	0.22	-	-	4/1	0.07	-	15.3
<i>P. fusina</i>	6/0	-	40	1.33	1/0	0.83	-	-	-	22.0
<i>N. xanthaphes</i>	1/0	-	10	0.22	-	-	1/1	0.03	-	16.3
<i>A. duma</i>	2/0	1/0	30	0.67	2/0	1.67	-	-	-	21.1
<i>A. aegita</i>	1/0	-	10	0.22	-	-	4/0	0.05	x	22.6
<i>S. triangularis</i>	-	2/0	10	0.44	1/0	0.83	-	-	-	20.7
<i>S. esperi</i>	2/0	1/0	30	0.67	1/0	0.83	3/1	0.05	-	17.0
<i>S. saladin</i>	2/0	-	10	0.44	1/0	0.83	0/3	0.04	-	25.2
<i>S. salius</i>	4/0	-	20	0.89	1/0	0.83	4/0	0.05	-	24.3
<i>T. thrasea</i>	2/0	-	20	0.44	2/0	1.67	1/0	0.01	-	22.2
<i>N. seron</i>	1/0	1/0	20	0.44	-	-	-	-	x	20.7
other spp.	-	-	-	-	6/0	5.00	-	-	-	-

TABLE 2. Abundance of Hesperidae at army ant swarms, paper lures, and during general collecting in Rondônia, Brazil.

	<i>Eciton</i>	<i>Labidus</i>	total ants	lures	general
males/hour	10.21	12.35	10.76	5.67	0.69
females/hour	0.33	0.09	0.27	0.08	0.23
male:female	342:11	142:1	485:12	62:1	527:174
percent males	97	99	98	98	75
no. of species	94	56	110	34	69

TABLE 3. Comparison of abundance and presence in traps and at paper lures of three groups of army ant associated Hesperidae in Rondônia. Number of species not taken during general collecting is indicated in parentheses.

group	no. of species	abundance (no./hour)		% species in traps	% species at lures
		with ants	without ants		
common species	22 (1)	6.84	0.29	86	68
same abundance	12	0.38	0.48	17	8
others	76 (39)	3.80	0.14	20	24

Others (identified by distinctive wing chips) returned several times to the swarm during the course of the day.

We did not specifically study the behavior of skippers at bird droppings because at the time we were more interested in species diversity and abundance. Two observations, however, are of note. First, all species perched at droppings (and lures) had their proboscis extended onto the fecal mass (or lure) indicating that they were feeding. Second, some individuals perched on a leaf with their abdomen above the droppings or lure. These latter may have been excreting fluid to rehydrate a dry dropping (see Roever, 1964, Hessel, 1966, Adler, 1982).

A few other butterfly species were at army ant swarms during our studies but their numbers and frequencies were low. The most persistent was *Tigridia acesta* (Linnaeus) (Nymphalidae) which was noted (as one or two individuals) feeding at bird droppings (and our lures) at all except one of the *E. burchelli* (but not *L. praedator*) swarms we studied. One individual of another nymphalid, *Pyrhogyra amphiro* Bates, visited bird droppings and lures at one swarm of *E. burchelli*. Occasional ithomiine species

(particularly *Mechanitis* spp.) were also seen at *Eciton* swarms. There were never more than three or four ithomiines in attendance; they fed at bird droppings; and only rarely investigated our lures.

DISCUSSION

The occurrence of butterflies at swarms of army ants has been sparsely reported in the literature. Drummond (1976) apparently was the first to note this phenomenon after he found males of a *Graphium* (= *Eurytides*, Papilionidae) and females of two species of *Mechanitis* (Nymphalidae: Ithomiinae) associated with a swarm of *Eciton burchelli* in Honduras. He suggested that the "army ant odor" (pheromones) was similar to that of male ithomiines (thus attracting females) or stimulated food searching behavior in the the papilionid. Young (1977) replied that the "odor of decay" of ant swarms provided a nutrient source attraction, observing that ithomiine butterflies often feed at bird droppings.

Ray and Andrews (1980) studied the association of three ithomiine species with bird droppings at *Eciton burchelli* swarms in Costa Rica. Although overall behavior of these was similar to that of the skippers in our study, several differences aside from the diversity of taxa were obvious. Their most abundant species, *Mechanitis polymnia*, occurred at an average of 2.9 individuals per hour; our most abundant species, *Astrartes fulgurator*, was less than half as common at 1.2 individuals per hour. Their three species, however, averaged 5 individuals per hour less than half the total abundance of skippers (11 per hour) in Brazil (Table 2). The striking difference was in the sex ratios of the two samples. The ithomiine association was a significantly female-biased phenomenon (91% females, 17:170). Female ithomiines occurred with ants at 13 times their abundance in similar situations without ants; males occurred at similar abundances both with and without ants. We found the opposite for ant associated skippers (98% males, 485:12) with males 15 times as abundant as away from ants and females at about the same abundance in both situations (Table 2).

Skippers are known to be attracted to bird droppings (Downes, 1973). We have often noted skippers (mainly large species) visiting droppings of birds in the Neotropics. It is obvious that this material contains an important or essential nutrient (Ray and Andrews, 1980), probably nitrogen, and possibly moisture for at least certain taxa. It is also known that male Lepidoptera greatly

TABLE 4. Taxonomic composition by subfamily and size of Hesperidae associated with army ants in Rondônia, Brazil.

	number (%) of species		% individuals with ants	% fauna associated with ants	mean size (mm)		
	total fauna	with ants			total fauna	with ants	without ants
Pyrrhopyginae	13 (3.1)	2 (1.8)	0.4	15.4	24.2	26.9	23.6
Pyrginae	243 (58.7)	80 (72.7)	89.3	32.9	19.4	22.3	18.0
Hesperinae	158 (38.2)	28 (25.5)	10.3	17.7	16.0	20.1	15.0
Total	414 (100)	110 (100)	100.0	26.6	18.3	21.8	16.9

outnumber females at water, feces, and other salt sources (Collenette, 1934; Norris, 1936; Downes, 1973; Arms *et al.*, 1974; Adler, 1982). Damp soil and animal excreta were suggested as important sources of sodium and amino acids for male butterflies (Arms *et al.*, 1974; Adler and Pearson, 1982); feces of carnivores are preferred to those of herbivores (Sevastopulo, 1974; pers. obs.). It has long been thought that skippers search for salt (Poulton, 1917); this was confirmed by Pivnick and McNeil (1987) who found all individuals of the hesperiine *Thymelicus lineola* (Ochsenheimer) at water were males. Male *Agathymus* skippers (Megathyminae) feed at wet earth and fresh feces but females apparently do not feed (Roever, 1964).

Nitrogenous nutrients (at least amino acids) are of importance for the production of eggs in butterflies (Dunlap-Pianka *et al.*, 1977). In many species, these compounds are sequestered by the larvae (Scriber and Slansky, 1981) but in others they are almost exclusively obtained by the adults (Gilbert, 1972). The importance and dynamics of adult foraging has not been studied extensively yet is known to be important in the reproductive biology of several species (Stern and Smith, 1960; Gilbert, 1975; Boggs *et al.*, 1981) and apparently plays an important role in determining butterfly use of time and space (Gilbert and Singer, 1973; Ehrlich and Gilbert, 1973; Murphy, 1983; Murphy *et al.*, 1984). Females forage at nitrogen sources in some taxa (Gilbert, 1972; DeVries, 1979; Ray and Andrews, 1980). Males of other taxa apparently provide significant nitrogen to females at copulation via spermatophores (Thornhill, 1976; Boggs and Gilbert, 1979; Boggs, 1981; Boggs and Watt, 1981). Similarly, sodium is of importance in the reproductive biology of butterflies. Males may transfer a third of their abdominal sodium to the female through the spermatophore and females may use half or more of their total body sodium in the production of eggs (Adler and Pearson, 1982; Pivnick and McNeil, 1987). Male sodium levels at emergence are different from those of females and deplete more rapidly (Adler and Pearson, 1982; Pivnick and McNeil, 1987). Access to sodium and amino acids positively affects mating success and spermatophore size in male butterflies and reproductive success of females impregnated by such males (Pivnick and McNeil, 1987; Lederhouse *et al.*, 1990). Bird droppings provide both renal and digestive wastes and may serve as a source of both sodium and nitrogen. Bird droppings have been suggested as a source of uric acid, amino acids, and other nitrogen compounds for ithomiines (Andrews, 1983).

Our data suggest a fundamental difference in the biology of ithomiines and hesperiids. Female ithomiines apparently obtain their nutrients directly. Female skippers, on the other hand, apparently do not obtain these directly from bird droppings. Males forage on droppings either as a nutrient source for their own maintenance or collect nutrients to pass on to females at mating. Visiting droppings for water seems unlikely since water is generally available in the tropics. Since some individuals were seen apparently rehydrating dried droppings, soluble materials are probably derived (e.g., Arms *et al.*, 1974).

Ithomiines sequester pyrrolizidine alkaloids for production of pheromones and as a protective chemical (Boppre, 1984). They also form mixed-species leks for mating (DeVries, 1987). These are both male dominated activities (Ray and Andrews, 1980; Andrews, 1983). Thus, allocation of time for foraging at nutrient

sources by male ithomiines may be constrained by these other activities making it necessary that females forage for nutrients needed for egg production. Adults of hesperiids are not known to sequester alkaloids or form leks as do ithomiines. Such differences possibly account for the opposite sex ratios of these two groups at bird droppings.

Ray and Andrews (1980) suggested that because of possible predation by the birds associated with army ant swarms, only unpalatable butterflies and their mimics could use this bird dropping resource. We know of no information on the palatability of hesperiids but cannot disprove that some species may be unpalatable. Hesperine skipper larvae feed on a variety of monocots and are probably palatable. Pyrrhopygines and pyrgines feed as larvae on dicots and it is possible that some sequester compounds making them distasteful to vertebrates. The resemblances between members of several, often disparate, genera of all three subfamilies are suggestive of this possibility. Striking examples at Fazenda Rancho Grande include the red-banded *Aspitha* (Pyrrhopyginae) and *Tarsoctenus* (Pyrginae); the blue-striped *Elbella*, *Jemadia* (both Pyrrhopyginae), *Phocides*, and female *Tarsoctenus corytus* (both Pyrginae); the large black (or black with white hyaline spots) *Pyrrhopyge*, *Elbella* (both Pyrrhopyginae), *Phocides* (Pyrginae), and *Thracides* (Hesperinae); and the black and bright blue (often with white hyaline spots) *Astrartes* (Pyrginae), *Thracides*, *Neoxeniades*, and *Aroma* (all Hesperinae). It is more probable that the powerful flight of most of these species allows escape from potential predators (e.g., Marden, 1992).

We do not as yet know the dynamics of the ant-bird-butterfly association but it is tempting to speculate. We know that the ants flush prey eaten by a number of ant associated birds and that bird droppings are visited by various butterflies. Our observations establish that the ultimate attraction of skippers to swarms of army ants is for feeding from bird droppings. The proximate factors involved are less clear. Certain ant associated birds, at least, daily search for and follow ant swarms (Willis, 1967a). The mechanism by which skippers locate ants is unknown but there is more than one possibility: 1) skippers may continually search for bird droppings and then remain in an area where the concentration is high, 2) they may be attracted chemically to ant swarms, or 3) once encountered, ant swarms may be followed for days at a time. Downes (1973) suggested that foraging areas of butterflies were discovered by odor and, in the case of bird droppings, perhaps vision. Drummond (1976) and others have noted the distinctive odor of army ant swarms. We have seen large numbers of bird droppings at ant swarm fronts, along their columns and in the vicinity of bivouacs. Willis (1967a) noted that the droppings of *Gymnopithys bicolor* (Formicariidae) are white and fluid, excreted frequently, and that ant swarms can be followed through the forest by a trail of excreta on the ground and low-growing leaves. Such a trail is left by birds attending a swarm as it advances. Additional droppings are left behind the main swarm by subordinate species in the hierarchy established when there is a multispecies bird flock present (Willis, 1972a). There is even likely to be a concentration of bird droppings at a bivouac that is not swarming. Willis (1967a, 1972a, 1982b) noted several bird species repeatedly investigating inactive bivouacs.

Data from our control observations (saliva-moistened paper

away from ants) and general collecting suggest more than one of these possibilities may be real and that different skipper taxa locate ants differently. Certain species of ant associated skippers are attracted to paper lures and others apparently are not (Tables 1, 2). These are largely the same species that are generally seen away from lures and droppings (many are also found in traps baited with putrid fish) indicating that they are widely distributed in the forests studied. The comparative numbers caught demonstrates a concentrating effect of the ant swarms (or associated bird droppings).

This is obviously a preliminary report on mixed-species aggregations of hesperiid butterflies in the vicinity of army ant swarms and adds one more group of animals directly or indirectly associated with their activities. These form to take advantage of a superabundant nutrient source in the form of the droppings of ant associated birds. This behavior by skippers is apparently not widespread as it has not been reported in the literature on ants (Hölldobler and Wilson, 1990) nor by those who studied ithomiine association with ants in Central America (Drummond, 1976; Ray and Andrews, 1980). We have documented the large number of species and individuals that may be found at ant swarms. There are many aspects of this association that remain to be investigated. These include methods of locating swarms, daily and long term fidelity of individuals to an ant swarm, specific differences in behavior in the use of the nutrient source, daily and seasonal activity patterns, inter- and intraspecific relationships among the species involved, and the significance of this behavior in the overall life histories of the various skipper species.

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APPENDIX I. Nomenclature of the HesperIIDae associated with army ants in Rondônia, Brazil (* indicates additional *Eciton* associated species during the 1991 study but not at swarms included in tables).

PYRRHOPYGINAE

Pyrrhopyge rubricollis (Sepp)
**Pyrrhopyge amythaon polka* Evans
Elbella patrobas (Hewitson)

PYRGINAE

Tarsoctenus corytus (Cramer)
Tarsoctenus praecia (Hewitson)
Phanus vitreus (Stoll)
Phanus species
Phanus obscurior Kaye
Phanus marshallii Kirby
Udranomia kikkawai (Weeks)
Augiades criniscus (Stoll)
Hyalothyruis infernalis (Möschler)
Hyalothyruis neleus (Linnaeus)
Epargyreus clavicornis (Herrich-Schäffer)
Epargyreus socus Hübner
Epargyreus exadeus (Cramer)
Aguna asander (Hewitson)
Aguna aurunce (Hewitson)
Aguna coelus (Stoll)
Aguna hypozonius (Plötz)
Aguna species
Aguna metophis (Latreille)
Typhedanus optica Evans
Polythrix auginus (Hewitson)
Heronia labriaris (Butler)
Chrysoplectrum otriades (Hewitson)
Chrysoplectrum perniciosus (Herrich-Schäffer)
Chrysoplectrum pervivax (Hübner)
Urbanus pronta Evans
Urbanus esta Evans
Urbanus belli (Hayward)
Urbanus esmeraldus (Butler)
Urbanus acawoios (Williams)
Urbanus teleus (Hübner)
Urbanus carmelita (Herrich-Schäffer)
Urbanus chalco (Hübner)
Urbanus reductus (Riley)
Urbanus doryssus (Swainson)
Astrartes fulgurator (Walch)
**Astrartes aulus* (Plötz)
Astrartes halesius (Hewitson)
Astrartes apastus (Cramer)
Astrartes enotrus (Stoll)
Astrartes janeira (Schaus)
Astrartes alardus (Stoll)
Astrartes alector (Felder & Felder)
Astrartes latimargo (Herrich-Schäffer)
Astrartes anaphus (Cramer)
Narcosius parisi (Williams)
Narcosius colossus (Herrich-Schäffer)
Narcosius nazaraeus Steinhauser
Narcosius species
Calliades zeutus (Möschler)
Cephise species
Autochton longipennis (Plötz)
Autochton zarex (Hübner)

Autochton neis (Geyer)
Dyscophellus euribates (Stoll)
Nascus phocus (Cramer)
Nascus solon (Plötz)
Porphyrogenes vulpecula (Plötz)
Porphyrogenes spanda Evans
Porphyrogenes suva Evans
Porphyrogenes species
Ablepsis amazonensis (Bell)
Spathilepia clonius (Cramer)
Marela tamyroides (Felder & Felder)
Telemiades delalande (Latreille)
Telemiades squanda Evans
Telemiades nicomedes (Möschler)
Telemiades epicalus Hübner
Telemiades penidas (Hewitson)
Pyrdalus corbulo (Stoll)
Spioniades artemides (Stoll)
Quadrus fanda Evans
Pythonides jovianus (Stoll)
Milanion pilumnus Mabilie & Bouillet
Charidia lucaria (Hewitson)
Aethilla echina Hewitson
Achlyodes busirus (Cramer)
Grais stigmaticus (Mabilie)
Anastrus obscurus Hübner
Camptopleura impressus (Mabilie)
Cycloglypha enega (Möschler)

HESPERIINAE

Synapte silius (Latreille)
Venas caeruleans (Mabilie)
Papias proximus (Bell)
Cobalopsis nero (Herrich-Schäffer)
Vettius phyllus (Cramer)
Naevolus orius (Mabilie)
Vertica verticalis (Plötz)
Dubiella dubius (Stoll)
Tellona variegata (Hewitson)
Damas clavus (Herrich-Schäffer)
Carystoides basoches (Latreille)
Carystoides noseda (Hewitson)
Carystoides lebbaeus (Hewitson)
Carystoides orbius (Godman)
Carystoides cathaea (Hewitson)
Perichares deceptus (Butler & Druce)
Orses cynisca (Swainson)
Decinea lucifer (Hübner)
Panoquina fusina (Hewitson)
Niconiades xanthaphes Hübner
Aides duma Evans
Aides aegita (Hewitson)
Saliana triangularis (Kaye)
Saliana esperi Evans
Saliana saladin Evans
Saliana salius (Cramer)
Thracides thrasea (Hewitson)
Neoxeniades seron (Godman)