BIOTROPICA 32(4a): 712–721 2000

Entomophagy, Behavior, and Elongated Thoracic Legs in the Myrmecophilous Neotropical Butterfly *Alesa amesis* (Riodinidae)[1]

P. J. DeVries[2] and **C. M. Penz**[2]
Department of Biology, University of Oregon, Eugene, Oregon 97403, U.S.A.

ABSTRACT

Entomophagy in the riodinid butterfly tribe Eurybiini is demonstrated for the first time. *Alesa amesis* caterpillars and adults possess behavioral and morphological traits for feeding on Homoptera nymphs, and oviposition by *A. amesis* females is mediated by the combined presence of *Camponotus femoratus* ants and homopteran nymphs. Caterpillars are entirely entomophagous, and do not eat plant tissues. *Alesa amesis* caterpillars have distinct behaviors for feeding on their prey, and for soliciting and drinking honeydew secretions from homopteran nymphs. The leg lengths of entomophagous *Alesa* caterpillars are shown to be longer than phytophagous relatives. The legs of *Alesa* are used for prey handling and soliciting honeydew secretions. We suggest that elongation of the thoracic legs has been a general consequence of entomophagy in butterfly caterpillars. This study clarifies our understanding of *A. amesis* and its interactions with multiple species, and points to behavioral and morphological traits important to interpreting the evolution of entomophagy among caterpillars. Our observations establish the likelihood that other members of Eurybiini may be entomophagous, and suggest that entomophagy may have evolved independently among the Nymphidiini and Eurybiini.

RESUMEN

Nuestro estudio presenta la primera documentación de entomofagia en la tribu Eurybiini. Las larvas y adultos de *Alesa amesis* tienen características morfológicas y de comportamiento que facilitón su alimentación de ninfas de Homoptera y, en esta especie, la oviposición se effectua bajo la presencia conjunta de hormigas *Camponotus femoratus* y ninfas de homopteros. Las larvas de *A. amesis* son entomófagas y no comen materia vegetal. Además, las larvas tienen comportamientos distintos para alimentarse de su presa y para solicitar y beber secreciones producidas por las ninfas de homopteros. Demonstramos que las piernas torácicas de las larvas entomófagas de *Alesa* son más largas que las de especies fitófagas cercanas. Las larvas de esta especie usan sus largas piernas para manusear y solicitar secreciones de homopteros. Proponemos que el alargamiento de las piernas torácicas es una consecuencia general de la entomofagia en larvas de mariposas. Nuestro estudio clarifica el conocimiento de la interacción entre *A. amesis* y otras especies de insectos. Además, discutimos características morfológicas y de comportamiento importantes para el estudio de la evolución de la entomofagia en larvas de mariposas. Se establece la posibilidad que otras especies de Eurybiini pueden ser entomofagas y se sugere que especies de Eurybiini y Nymphidiini evoluiran hábitos entomófagos independientemente.

Key words: Alesa; *entomophagy; Eurybiini; leg elongation; membracid nymph; obligate myrmecophily; secretion feeding; Riodinidae; symbioses.*

THE ABILITY OF INSECTS TO FORM SYMBIOSES WITH ANTS (termed myrmecophily) is best known among the Homoptera and Lepidoptera. In these symbioses, both myrmecophilous Homoptera and Lepidoptera typically provide ants with food secretions in exchange for protection against predators and parasitoids (Way 1963; Cottrell 1984; Buckley 1987; Pierce 1987; DeVries 1988, 1991a, 1997; DeVries & Baker 1989; Buckley & Gullen 1991; Fiedler 1991). Among butterflies, myrmecophily occurs only in the Lycaenidae and the Neotropical Riodinidae. Due to the strong influence on fitness (*e.g.*, Pierce *et al.* 1987, DeVries 1991a, Wagner 1993, Wagner & Martinez del Rio 1997), caterpillars maintain constant ant attendance through the use of several specialized organs that produce food secretions, semiochemicals, and substrate-borne calls that modify ant behaviors and enhance symbioses with ants (Cottrell 1984; DeVries 1988, 1990, 1997; Fiedler *et al.* 1996).

Phytophagy among butterfly caterpillars is so pervasive that the relationships between butterflies and their specific host plants formed the basis for the predictive concept of coevolution between insects and plants (Ehrlich & Raven 1964). In con-

[1] Received 28 May 1999; revision accepted 1 November 1999.

[2] Current address: Center for Biodiversity Studies, Milwaukee Public Museum, 800 West Wells St., Milwaukee, Wisconsin 53233, U.S.A.

trast, entomophagy (the habit of feeding on insects) by butterfly caterpillars is rare, and well known only among the myrmecophilous lycaenids, particularly the Liphyrinae and Miletinae of the Old World tropics (Cottrell 1984, Ackery 1990, Pierce 1995).

Insights into the complexity of entomophagous lycaenid life cycles began with the basic observations of Lamborn (1915), Farquarson (1922), Jackson (1937), and Cripps and Jackson (1940) on African Miletinae, and recently reached an elegant benchmark with studies on European *Maculinea* (Polyommatinae) and ants in the genus *Myrmica* (Thomas *et al.* 1989, Elmes & Thomas 1992, Thomas & Wardlaw 1992, Akino *et al.* 1999). Although complex multispecies interactions likely occur in a variety of entomophagous lycaenids (Owen 1971, Henning 1983, Cottrell 1984, Johnson & Valentine 1986, Kitching 1987, Maschwitz *et al.* 1988, Banno 1990, Pierce 1995), the majority have not been studied in detail. In contrast to the lycaenids, only one species of riodinid has been documented as being entomophagous; the caterpillars of *Setabis lagus* feed on the nymphs of Homoptera (DeVries 1997). In sum, relatively little is known about the complexity of interactions between most entomophagous butterfly caterpillars and other species.

The riodinid tribe Eurybiini currently includes 24–31 species in three genera: *Eurybia* (20–25 species), *Alesa* (4–5 species), and the monobasic *Mimocastnia* (Harvey 1987, Bridges 1994, Hanner 1998). Based on the close relationship among genera and rearing records from one genus, all Eurybiini are considered to be myrmecophilous (Harvey 1987). The number of observations on Eurybiini caterpillars, however, is relatively small. Of 20 or more *Eurybia* species, only 8 have been confirmed as herbivores on flowers of Marantaceae or Zingiberaceae (*e.g.*, Horvitz *et al.* 1987; DeVries *et al.* 1994; DeVries 1997; DeVries, pers. obs.); the rest are unknown.

The butterfly *Alesa amesis* (Cramer) is a widespread and often common species of Eurybiini ranging from Colombia, Venezuela, the Guianas, Ecuador, and Peru south through the Amazon basin of Brazil. The only information on the early stages of *Alesa* has come from Harvey (1987), who cited J. Mallet (pers. comm.) as having found an undetermined *Alesa* caterpillar tended by *Crematogaster* sp. (Myrmicinae) ants on *Solanum* sp. (Solanaceae). Based on well established patterns of host plant association in butterflies (Ehrlich & Raven 1964) and host records from its sister genus *Eurybia*, our previous understanding of *Alesa* caterpillars was that they are myrmecophilous and phytophagous (*e.g.*, Harvey 1987, Brown 1993).

During a long-term investigation of butterfly diversity in a lowland Ecuadorian forest, we studied *A. amesis* in some detail, and in contrast to previous suggestions, found that the caterpillars were entirely aphytophagous. We present the first documentation of entomophagy in the Eurybiini, and show that *A. amesis* caterpillars and adults possess behavioral and morphological traits that facilitate feeding on Homoptera. First, we summarize our field observations on *A. amesis* to provide a narrative pertinent to understanding this butterfly in the context of myrmecophily and entomophagy. Second, we compare *A. amesis* with other riodinid species using comparative allometric data to determine the effect entomophagy has had on caterpillar leg lengths, and discuss our findings to make several predictions regarding the evolution of entomophagy in butterfly caterpillars.

METHODS

Field observations were conducted intermittently on *A. amesis* from July 1994 through July 1998 at the La Selva Lodge, Garza Cocha, Sucumbios, Ecuador (hereafter LSL), where dominant habitat types included intact lowland floodplain forest, areas of riparian forest, and small patches of second-growth vegetation occurring around human habitation. A more detailed description of the field site is found in DeVries, Walla *et al.* (1999).

Oviposition, interactions with ants, and larval feeding behaviors were observed in the field, or on field-collected individuals that were brought to a laboratory and confined in plastic containers or on potted plants at ambient temperatures. Early instars were placed in Quinter's solution, transferred to 70 percent alcohol for storage (protocol in DeVries 1997), and subsequently examined with light microscopy. Terminology for caterpillar morphology pertinent to myrmecophily follows Cottrell (1984).

The calls of *A. amesis* caterpillars were detected and recorded with a Bennet-Clark (1984) particle velocity microphone using the methods described in DeVries (1991c). Subsequently, calls were characterized using the sound analysis program Canary version 1.2.

Field observations suggested that the thoracic legs of *A. amesis* caterpillars were relatively longer than those of other riodinid genera. To test this hypothesis, we compared leg lengths of *A. amesis* caterpillars to those of 31 riodinid caterpillars rep-

resenting 21 species, 18 genera, and 8 tribes, as defined by Harvey (1987) and Penz and DeVries (1999). For each specimen, the length of the femur, tibia, and tarsus of one leg on each thoracic segment, and head width were measured using an ocular micrometer. To compare leg lengths among taxa, the head width of each specimen was used as a standard measure of size, and the sum of each leg length (minus claw) was plotted against head width. For each thoracic leg, a regression line was fitted through points representing 21 riodinid species, and then points representing *A. amesis* were overlaid on the graphs.

RESULTS

ADULTS.—*Alesa amesis* adults were present during the 48-month observation period, but abundance was lowest in the driest months, a pattern common in many other butterfly species (DeVries *et al.* 1997; DeVries, Lande *et al.* 1999; DeVries, Walla *et al.* 1999; DeVries, pers. obs.). On sunny days, *A. amesis* males (N = >100 observations) perched in light gaps and along streams and trails 0.5–3.0 m above the ground between 0800 and 1620 h, with peak perching activity from 1000 and 1500 h. Females flew between 0900 and 1420 h, but oviposition behavior was observed only between 1130 and 1420 h on sunny days. Between 0800 and 1000 h, both males and females were frequently seen visiting flowers of *Psiguria* sp. (Cucurbitaceae) that occurred in light gaps and along edges, but never visiting the flowers of any other plant.

OVIPOSITION BEHAVIOR.—Direct observation of >60 individual oviposition events showed that female *A. amesis* deposited single eggs on a variety of plant species; however, oviposition occurred only in the presence of the formicine ants *Camponotus femoratus* (Fabricius) that were vigorously tending groups of Membracidae nymphs. Also present at all oviposition events was the ant *Crematogaster* nr. *parabiotica* (Myrmicinae) which always was associated with *C. femoratus* foraging trails (see Discussion). Most oviposition events occurred immediately adjacent to membracid aggregations located at the distal ends of branches that bore new shoots or flower buds. Oviposition occurred less frequently near aggregations located on woody branches, and occasionally, directly on individual membracid nymphs (Fig. 1a). In summary, we observed female *A. amesis* ovipositions near aggregations of three genera of Membracidae that were tended by *C. femoratus* ants, and these oviposition events occurred on seven plant genera representing five families (Table 1).

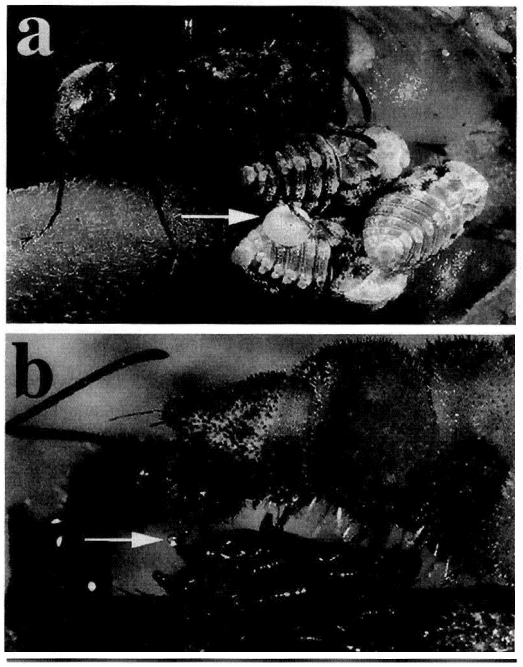

FIGURE 1. Early stages of *Alesa amesis*. (a) Egg laid directly on a membracid nymph (arrow). An individual *Camponotus femoratus* ant is tending this group of membracids. (b) Close-up of a mature *A. amesis* caterpillar about to drink a drop of honeydew (arrow) produced by a membracid nymph. Note that the caterpillar legs were used to solicit the drop of honeydew. An individual *C. femoratus* ant is visible to the left and behind the caterpillar.

Oviposition behavior in *A. amesis* varied, depending on individual butterflies, individual plants, time of day, and degree of direct sunshine, but a general overview of oviposition behavior is as follows. Females were frequently observed fluttering around aggregations of membracids composed of adults and/or nymphs tended by *C. femoratus* ants. After hovering close to an ant–membracid aggregation, a female typically would lurch forward, and while still airborne, touch the ants with its antennae several times. This behavior caused ants to become excited, but we never observed ants attempting to attack the butterflies. After antennating the ants, the female would land adjacent to the membracid aggregation and rapidly deposit a single egg. Oviposition typically took three seconds or less. After ovipositing, the females generally flew a short distance away and rested on the upper surface of a leaf with their wings open in full sunlight for a minute or more. Resting always occurred between

TABLE 1. *Summary of* Alesa amesis *oviposition events and host insects at La Selva Lodge. In all observations,* Camponotus femoratus *ants were tending aggregations of homopteran nymphs, and these nymphs were prey of* Alesa amesis *caterpillars. Abbreviations: Plant part (yl = young leaves; ol = old leaves; fb = flower buds; ns = new shoots; and f = fruit) and* N *= number of oviposition events observed.*

Plants	*N*	Plant part	Homopteran taxon
Grias sp. (Lecythidaceae)	1	f	Atelionidae undet. sp.
	3	ns	*Horiola* sp.
Serjania sp. (Sapindaceae)	6	yl	*Apheta* sp.
Quararibaea sp. (Bombacaceae)	*ca* 10	fb	*Horiola* sp.
Citrus sp. (Rutaceae)	>15	yl, ol	*Horiola* sp.
Machaerium sp. (Fabaceae)	>10	yl, ns	*Horiola* sp.
Inga sp. (Fabaceae)	>5	yl	*Horiola* sp.
Swartzia sp. (Fabaceae)	>20	yl, ol	*Horiola* sp.
		yl	nr. *Notogonia* sp.

oviposition events. We observed female butterflies ovipositing repeatedly on individual plants that supported membracid aggregations on more than half of all terminal shoots, and occasionally individual females deposited up to ten eggs on the same plant. On plants bearing low densities of membracids and ants (<25% of shoots with aggregations of nymphs), oviposition behavior varied. Sometimes a female *A. amesis* would investigate a plant, deposit a single egg, and then move away. At other times, the female would fly away without ovipositing.

CATERPILLAR–ANT SYMBIOSIS.—Third and later instar *A. amesis* caterpillars were always found with *C. femoratus* ants in constant attendance. In marked contrast to *C.* nr. *parabiotica* ants, which showed no marked aggressive behaviors toward any other species, *C. femoratus* vigorously attacked any foreign arthropods and human observers that came near the caterpillars and homopterans they tended. In fact, regardless of whether or not they were tending caterpillars and homopterans, *C. femoratus* attacked any other animal species entering their territories or foraging trails.

Alesa amesis caterpillars have at least two traits that are important to myrmecophily. Like other myrmecophilous riodinids, *A. amesis* caterpillars possess a pair of eversible tentacle nectary organs (Fig. 2a, b, c) that produce food secretions critical to riodinid–ant symbioses (summaries in DeVries 1988, 1991a, 1997; DeVries & Baker 1989). Furthermore, all third and later instars produced substrate-borne calls, and a sample of eight *A. amesis* caterpillar calls (two 4th instars and six 5th instars) showed a mean pulse rate of 12.8/sec with call frequencies ranging from 300 to 1200 Hz, the most power between 750 and 800 Hz.

CATERPILLAR FEEDING ON MEMBRACIDS.—The diet of third and later instar *A. amesis* caterpillars included nymphs of three genera in Membracidae, and an unidentified Atelionidae (Table 1). Caterpillars fed intermittently on homopteran nymphs throughout 24-hour periods, always in association with ants. We found no evidence that any instars fed on plant material despite confining them with a "salad" of plant tissues originating from plants on which *A. amesis* early stages were found (Table 1). During 24 hours of confinement, the two first instars tested died, presumably of starvation. Other instars also refused to feed on plant material during 24 hours of confinement, but subsequently ate membracid nymphs when provided. Although second instars were not tested, these observations implied that *A. amesis* caterpillars may be aphytophagous in all instars.

When a foraging caterpillar encountered a group of membracids, it typically raised the head and thoracic segments above the substrate, and slowly began touching individual nymphs with the mouth and forelegs (Fig. 2a). In most instances when a nymph was approached in this manner, it moved away; however, nymphs in the premolt stage or those that somehow had acclimated to the presence of a caterpillar, did not move away. In these cases, a foraging caterpillar would arch over the nymph, and by repeatedly touching the substrate on either side of it, effectively restrain it with strands of silk (Fig. 2a and inset). After placing a few strands of silk over a nymph, the caterpillar then would arch over the nymph, seize it with the thoracic legs, and by curling its head down under the body, gather the nymph into the ventral concavity of the thorax and begin eating it (Fig. 2b, c). Here, the thoracic legs of *A. amesis* caterpillars appeared to play an important role in the subdu-

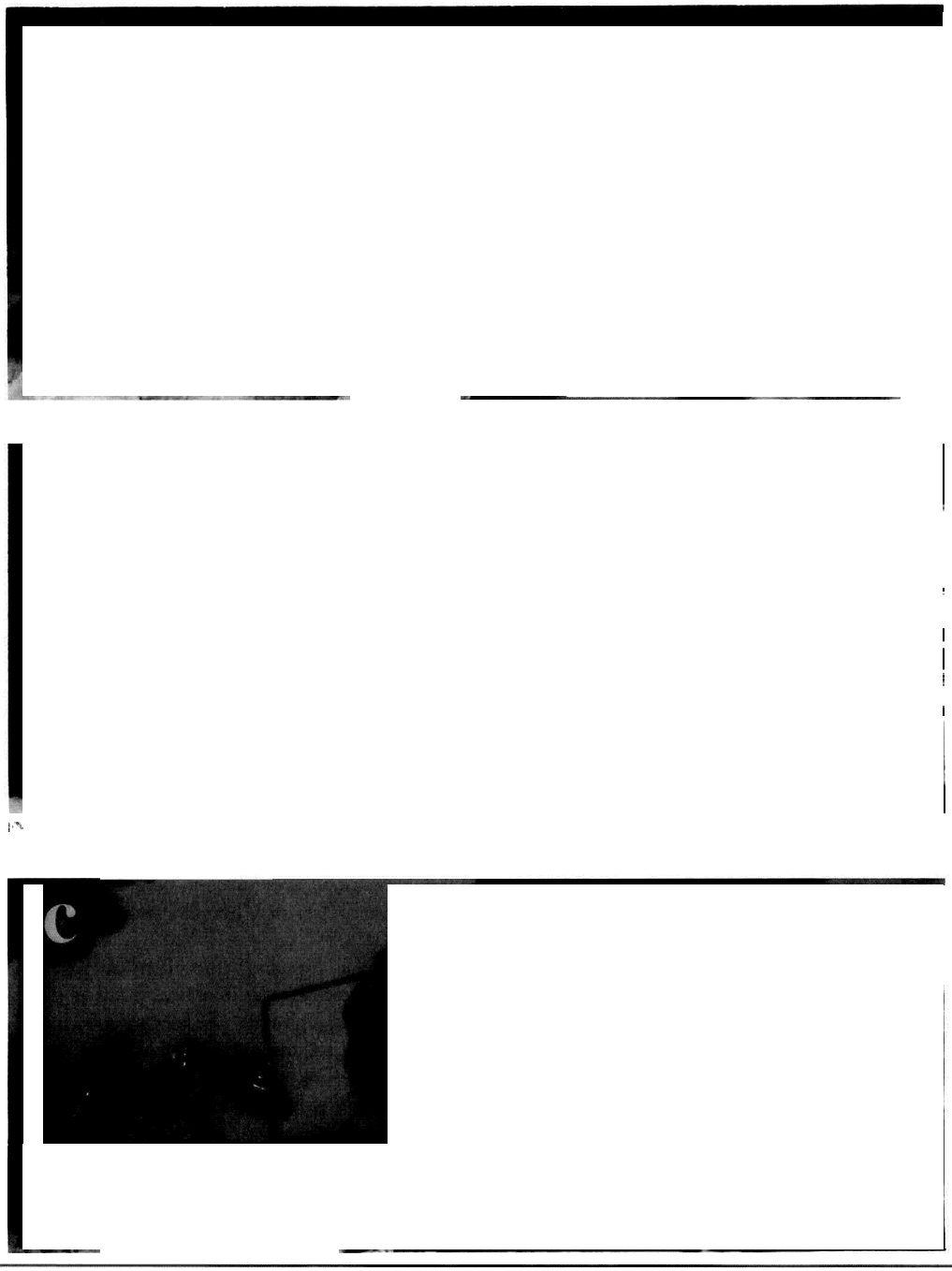

FIGURE 2. Feeding sequence of an *Alesa amesis* caterpillar. (a) The caterpillar using the thoracic legs to stroke a membracid nymph. The magnified inset shows the strand of silk running from the substrate near the forelegs of the membracid. Note that the anterior third of the caterpillar body is elevated above the nymph. (b) After grasping the membracid nymph, the caterpillar has begun to devour it. The caterpillar is being tended by an individual *Camponotus femoratus*. (c) Caterpillar after eating about one-half of the membracid nymph. The two ants are *Camponotus femoratus* (left) and *Crematogaster* nr. *parabiotica* on top of the caterpillar. Note that the orifice marking the position of the proximal tentacle nectary organ is clearly visible in all three figures.

ing, grasping, and eventual devouring of the membracid prey. Ants never interfered with caterpillars feeding on nymphs, even while continuing to tend other nymphs.

SECRETION FEEDING.—In addition to membracid nymphs, *A. amesis* caterpillars also fed on two types of secretions. On plant species bearing pronounced extrafloral nectaries (*e.g.*, *Inga* sp., *Machaerium* sp., and *Grias* sp.), caterpillars often rested with their heads over the nectaries, and presumably were drinking the nectar—a ubiquitous behavior among myrmecophilous riodinids (DeVries 1997). Caterpillars also drank honeydew produced by membracids. Frequently, we observed caterpillars touching membracid nymphs with their thoracic legs, and then drinking the drop of honeydew that appeared to result from the stimulation (Fig. 1b).

THORACIC LEG LENGTHS.—There was a positive relationship between caterpillar leg length and head width, showing that regardless of tribal affinity, larger riodinid caterpillars generally had longer legs than smaller caterpillars (Fig. 3). There were two exceptions. All legs of *A. amesis* fell well above the regression line, revealing that *Alesa* legs were relatively longer than those of comparative taxa (including its sister genus *Eurybia;* Fig. 3). The second and third legs in *S. lagus* paralleled those of *A. amesis; i.e.,* they were comparatively longer than those of other taxa in our sample. Finally, claw length was found to be greater in *Alesa* and *Setabis* than in all other taxa (DeVries & Penz, pers. obs.). There was one fundamental ecological difference in diet that separated *A. amesis* and *S. lagus* from other taxa in our sample. *Alesa amesis* and *S. lagus* caterpillars are entomophagous, whereas all other taxa are phytophagous (DeVries *et al.* 1994; DeVries 1997, pers. obs.). Although greater numbers of species will need to be surveyed, our observations suggest that entomophagy in riodinid caterpillars is correlated with an elongation of thoracic legs.

DISCUSSION

This study is the first to document obligate entomophagy in the tribe Eurybiini, and to show that *A. amesis* caterpillars and adults possess behavioral and morphological traits for feeding on Homoptera nymphs. Entomophagy among riodinid butterfly caterpillars was reported previously in only one species of *Setabis,* in the tribe Nymphidiini (Urich in Kaye 1921; DeVries 1997, pers. obs.). Therefore, our observations not only establish the likelihood that other members of Eurybiini may be entomophagous (other *Alesa* species and perhaps some *Eurybia*), but they also suggest that entomophagy may have evolved independently among the Nymphidiini (*sensu* Penz & DeVries 1999) and Eurybiini, tribes that appear to be distantly related (Harvey 1987).

Vibrational communication among ants can be a prevalent part of colony communication and recruitment (Markl & Hölldobler 1978, Baroni-Urbani *et al.* 1988, Hölldobler & Wilson 1990, Roces *et al.* 1995). The ability to produce substrate-borne calls bearing similarities to ant vibrational signals is widespread among myrmecophilous lycaenid and riodinid caterpillars (DeVries 1990, 1991b, pers. obs.), and these acoustical signals are believed to function in the enhancement and maintenance of symbioses with ants (DeVries 1990, 1991b, 1997; DeVries *et al.* 1993). It is probable that *A. amesis* calls enhance their symbioses with ants, and may even play a role in their interactions with membracids, because they also produce vibrational calls (*e.g.*, Ossiannilsson 1949). The frequencies and pulse rates we measured for *A. amesis* calls were closer to those of its sister genus *Eurybia* and lycaenid caterpillars than to those of riodinid caterpillars in the tribe Nymphidiini (DeVries 1991b). This situation likely was due to differences in the mechanism of call production between Eurybiini and Nymphidiini. Caterpillars in the Nymphidiini produce calls with vibratory papillae that function as a stridulatory mechanism (DeVries 1990, 1991b, 1997), whereas Eurybiini and all Lycaenidae lack vibratory papillae and the mechanisms of call production are unknown (DeVries 1991b, 1997).

Ant-mediated oviposition is known in several species of African and Australian lycaenids (Lamborn 1915, Jackson 1937, Pierce & Elgar 1985, Baylis & Pierce 1991) and Neotropical riodinids (summaries in DeVries 1997). Various Homoptera at LSL, including the Membracidae and Atelionidae that were known to be prey of *A. amesis,* frequently were tended by a variety of ant taxa (*e.g.*, *Dendromyrmex* spp., *Camponotus* spp., *Azteca* sp., *Megalomyrmex* spp., *Ectatomma* spp.); however, we only observed *A. amesis* adults ovipositing on, and caterpillars feeding on, Homoptera tended by *C. femoratus.* Thus we conclude that oviposition by *A. amesis* females was mediated by the combined presence of *C. femoratus* ants and homopteran prey, and that the symbiosis between *A. amesis* and *C. femoratus* is obligate.

Several adult and caterpillar behaviors shown by *A. amesis* converge on those described for Old

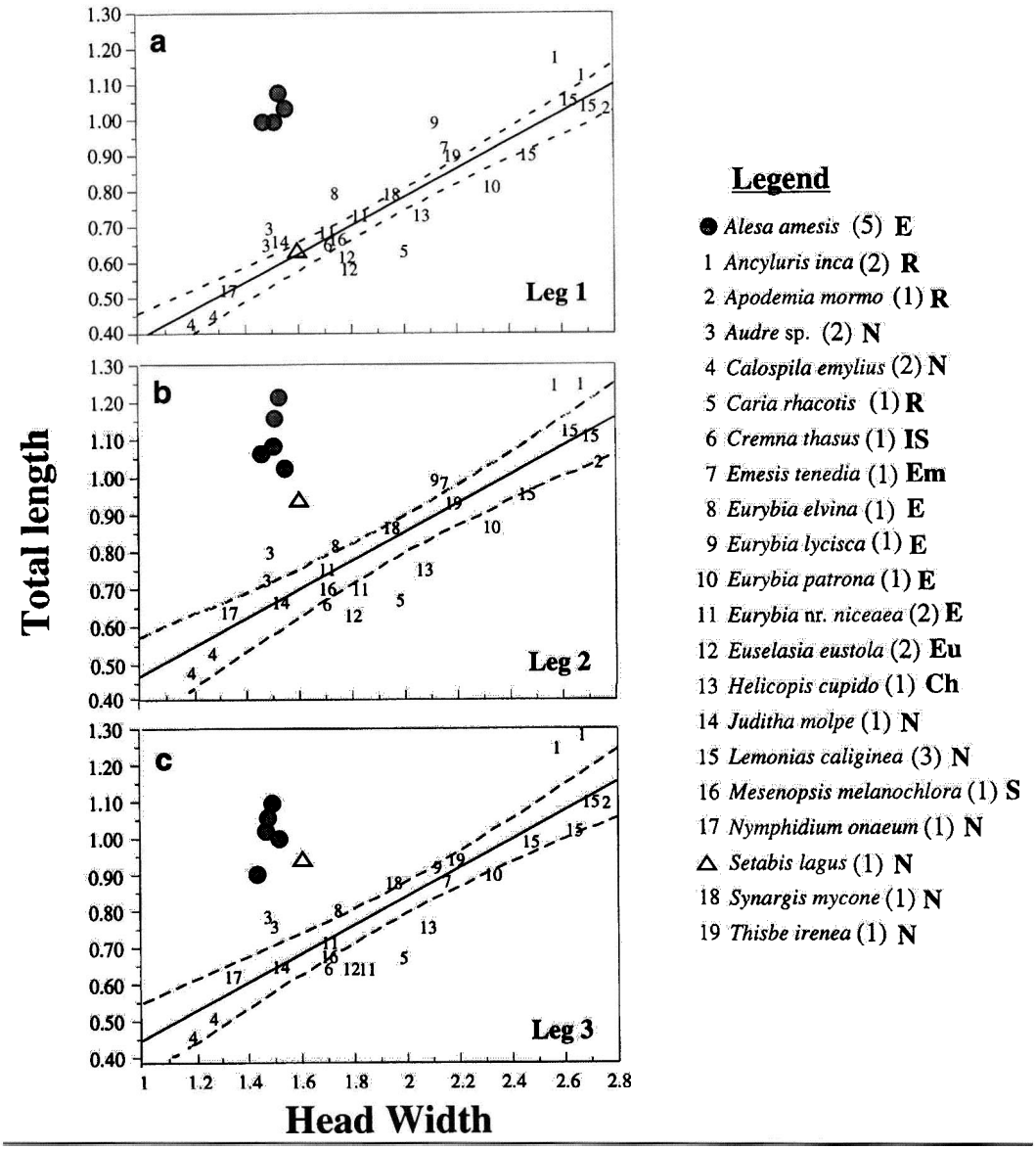

FIGURE 3. Relative length of thoracic legs of 22 species of riodinid caterpillars. (a) First thoracic legs. (b) Second thoracic legs. (c) Third thoracic legs. The sample size for each taxon in the legend is within parentheses. Abbreviations for the higher taxonomic categories by Harvey (1987) with modifications by Penz and DeVries (1999) are: **E** = Eurybiini; **R** = Riodinini; **N** = Nymphidiini; **IS** = Incertae Sedis; **Em** = Emesini; **Eu** = Euselasiinae; **Ch** = Charitini; and **S** = Symmachiini. All regressions were significant at $P < 0.005$. Note the longer legs of *Alesa amesis* in all plots, and the relatively longer legs of *Setabis lagus* for thoracic legs 2 and 3.

World lycaenids. The required presence of ants and aggregations of homopterans as a stimulus for oviposition is well known in the lycaenid subfamily Miletinae, including direct oviposition on homopteran nymphs (Cottrell 1984, Fiedler & Maschwitz 1989). Further, the behavior of *A. amesis* caterpillars arching over their prey prior to grasping and devouring them, and the habit of soliciting and drinking honeydew secretions from nymphs also has been reported from the miletine lycaenids *Lachnocnema, Spalgis,* and *Allotinus* (*e.g.,* Farquarson 1922, Jackson 1937, Clark & Dickson 1971). The supplemental growth benefits of drinking extrafloral nectar (DeVries & Baker 1989) and its

widespread occurrence among myrmecophilous riodinids (DeVries 1997) suggest that *A. amesis* (and lycaenid) caterpillars may benefit from drinking both honeydew and extrafloral nectar. The secretion feeding behavior described here has obvious parallels to the well-known behavior of ants that antennate Homoptera to solicit honeydew secretions (Hölldobler & Wilson 1990), and points to another function of the thoracic legs in *A. amesis* caterpillars. Although adult solicitation and feeding on honeydew secretion of Homoptera prey has been widely reported among the Old World Miletinae (*e.g.*, Cottrell 1984, Fiedler & Maschwitz 1989), we never observed it in *A. amesis* adults.

In many lowland Amazonian forests, *C. femoratus* colonies may occupy and dominate large territories (Davidson 1988). We found that these ants vigorously attack most arthropods and all vertebrates that get near or enter their foraging trails, territories, or food resources. Experimental work on caterpillar–ant symbioses (Pierce *et al.* 1987, DeVries 1991a, Wagner 1993) and the observations here strongly suggest that *A. amesis* caterpillars gain protection from predators through association with *C. femoratus*. Furthermore, the ability of *A. amesis* caterpillars to produce substrate-borne calls, in concert with the tentacle nectary organs, probably achieves and enhances the constant association of these caterpillars and their ant symbionts.

The term parabiosis signifies the symbiosis among two or more ant species that share the same nest and/or foraging trails, but which keep their brood separate (Forel 1898). As the name implies *C.* nr. *parabiotica* is parabiotic with other ant species throughout South America, especially in the large nests of *C. femoratus* (Davidson 1988). The only ant species we found constantly tending *A. amesis* caterpillars was *C. femoratus*, even though *C.* nr. *parabiotica* ants were invariably on or near caterpillars (Fig. 3). These observations open the possibility that the undetermined *Alesa* caterpillar reported by Mallet (in Harvey 1987) tended by *Crematogaster* could have been associated with *Camponotus* ants, but had become isolated from them prior to collection.

A general feature of many predators is the development of raptorial appendages. For example, disparate groups such as vertebrates in the Felidae and Falconidae, and invertebrates in the Mantidae, Mantispidae, Solpugidae, and Amblypigidae all show this characteristic. It has been suggested that caterpillars of *Lachnocnema bibulus* (Miletinae) have long legs (Farquarson 1922, Jackson 1937, Cripps & Jackson 1940) or claws (Clark & Dickson 1971) for grasping homopteran prey. More recently, Montgomery (1982) found that Hawaiian geometrid moth caterpillars of the genus *Eupethecia* had elongated thoracic legs armed with spike-like setae and claws that assisted in their ambush predation of small arthropods. The potential relationship between caterpillar entomophagy and leg length, however, has not been determined explicitly, or tested using quantitative comparative measures. We have demonstrated that caterpillar leg lengths of entomophagous *Alesa* and *Setabis* are longer than their phytophagous relatives (Fig. 3), and that elongated legs in *Alesa* are used for handling prey and soliciting honeydew secretions from membracids (Figs. 1 and 2). This study therefore provides quantitative and behavioral evidence from two distinct tribes suggesting that one consequence of entomophagy in riodinid butterfly caterpillars has been the evolution of elongated thoracic legs. Based on these observations, we predict that regardless of tribal affinity, elongated legs will be characteristic of entomophagous riodinid caterpillars, and we strongly suspect that many entomophagous lycaenid caterpillars may also have longer legs when compared to their phytophagous relatives.

Because many myrmecophilous riodinid caterpillars feed on plants with extrafloral nectaries, they are thought to be able to invade and exploit the interaction between secretion-producing plants and secretion-harvesting ants (DeVries & Baker 1989, DeVries 1991a). Our observations suggest that entomophagous riodinid species not only exploit the symbioses between ants and Homoptera, but also gain benefits from feeding on Homoptera honeydew and nymphs while being protected by ant symbionts.

This study has clarified and amplified our understanding of *A. amesis* and its interactions with multiple species, and has pointed to behavioral and morphological traits important to interpreting the evolution of entomophagy among butterfly caterpillars. In conclusion, we hope that our observations will stimulate interest in studying multispecies interactions among tropical butterflies.

ACKNOWLEDGMENTS

We extend thanks to the La Selva Lodge, its staff, and particularly Eric Schwartz, for providing the necessary field support. We thank T. K. Wood for determining Homoptera, J. Longino for identifying ants, J. Mallet for communications regarding old rearing records, and S. Collins, A. Heath, and A. M. Young for sending copies of critical literature. Voucher specimens of butterflies have been deposited in the collection of the American Museum

of Natural History, Universidad Catolica, and Museo de Ciencias (both in Quito), and that of PJD. Voucher material of host insects has been deposited with T. K. Wood (University of Maryland). The critical comments of P. R. Ackery, A. Aiello, M. Berger, H. Greeney, J. Longino, N. Martin, E. Scholes, T. Walla, and D. Wagner improved previous versions of this manuscript. We gratefully acknowledge the help of N. Gerardo, H. Greeney, and R. Hill in caring for early stages. DeVries wishes to thank the Guggenheim Foundation and MacArthur Foundation for supporting his recent research efforts. This study is dedicated to the symbiotic work of Sonny Clark, and George Duvivier, Kenny Dorham, and Paul Chambers, and Steve Lacy and J. J. Avenal.

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