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TRAIL-FOLLOWING BEHAVIOR AND NATURAL HISTORY OF THE SOCIAL CATERPILLAR OF *ARSENURA ARMIDA* IN COSTA RICA (LEPIDOPTERA: SATURNIIDAE: ARSENURINAE)

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ABSTRACT.– *Arsenura armida* (Cramer) is a large, social Neotropical saturniid caterpillar that is common in the tropical dry forest of the Area de Conservación Guanacaste in northwestern Costa Rica. This aposematic caterpillar feeds side-by-side in highly visible nomadic groups in the crowns of at least three distantly-related tree species in early instars. In the last two instars, it rests in equally visible groups on the tree trunks in the day while ascending to the tree crown to feed at night. This species may to be unique among arsenurines in exhibiting these traits; all known caterpillars of other species in this subfamily are cryptic, and none is known to be social. Laboratory studies show that larval trail-following is elicited by surface cuticular material collected by wiping from the venter and dorsum of the abdomen of *A. armida* caterpillars. Crude extracts of somatic tissue also elicited trail-following. This is the first published demonstration of pheromone-based trail-following by a saturniid. The long-lived trail marker used by this species appears to be a component of the cuticle and is passively deposited from the posterio-ventral region of the abdomen as larvae travel over the host plant. Unlike other social Lepidoptera such as tent caterpillars, these trails are not deposited on silk, but rather directly on the plant substrate. *A. armida* larvae are capable of discriminating between extract-derived artificial trails differing in strength by a factor of 2 or greater. The trail marker is highly persistent on paper. In the laboratory, a 24-hour-old trail is nearly as attractive as a freshly deposited trail.

KEY WORDS: Annonaceae, aposematism, behavior, biology, Bolivia, Bombacaceae, Brazil, Central America, chemical communication, *Ciao*, *Copiopteryx*, Diptera, *Dysdaemonia*, Guanacaste, hostplants, Hymenoptera, Ichneumonidae, immatures, larva, larval behavior, Lasiocampidae, *Malacosoma*, Mesoamerica, Mexico, Neotropical, oviposition, *Paradaemonia*, parasitoids, pheromones, *Rhesyntis*, social caterpillars, Sterculiaceae, Tachinidae, *Titaea*, trail pheromones.

At least 300 species of caterpillars found in 27 families of Lepidoptera are known to be social for part or all of their larval lives (Costa and Pierce, 1997). The mechanisms that social caterpillars use to maintain close physical contact have been investigated in a few of these species and have been shown to be based on pheromones either imparted to the caterpillar's silk as it is extruded (Roessingh, 1990; Fitzgerald, 1993b) or extra-silk markers secreted from the ventral surface of the tip of the abdomen and secondarily applied to deposited silk (Fitzgerald and Edgerly, 1982; Fitzgerald and Underwood, 1998a,b). In the most simple type of marking system described, caterpillars deposit silk continuously as they move over the substrate. The silk envelops the foliage upon which the caterpillars feed and a silk-associated pheromone that is detected with the contact chemoreceptors of the maxillae allows the colony to recognize the boundaries of the active foraging area and remain aggregated (Roessingh, 1990; Fitzgerald, 1993b). They apparently do not directly use the silk itself as a marker. The most elaborate substrate marking systems described so far are employed by holarctic tent caterpillars (Lasiocampidae: *Malacosoma* spp.). The larvae of several of these species are highly social and use a trail pheromone to recruit tentmates to food in a manner similar to that used by ants and termites (Fitzgerald, 1976, 1995).

Fitzgerald and Peterson (1988) suggested that social complexity in caterpillars is linked to foraging strategy. In particular, central-place foraging may set the stage for recruitment communication, the most sophisticated form of communication described in social caterpillars. Caterpillar communication is of great interest evolutionarily, as its most complex form (recruitment) incorporates the same elements of collective flexibility and group-level effects of individual decision making that figure so prominently in structuring eusocial hymenopteran societies (Fitzgerald and Costa, 1999).

A better understanding of recruitment communication and its likely ecological correlates and behavioral antecedents in other forms of trail-following behavior holds great promise for providing insights into general principles of social evolution. The foraging systems of most social caterpillar taxa, whether based on pheromones or other mechanisms, remains to be described, however. We currently have little knowledge of the range of marking and other social behaviors employed by the great majority of social caterpillars, and are in need of descriptions of the social ethology of a broad range of taxonomically distinct caterpillar species. To this end, we examined the larval trail-following behavior of *Arsenura armida* (Cramer) (Saturniidae). Pheromone-based foraging behavior has not been previously investigated in the Saturniidae despite the occurrence of numerous social species in at least three saturniid subfamilies worldwide (Costa and Pierce, 1997; D. H. Janzen, pers. obs.). *A. armida* is especially interesting in that it may represent the only example (or, more likely, one of very few examples) of larval sociality in the subfamily Arsenurinae (D. H. Janzen, pers. obs.).

OVERVIEW OF *ARSENURA ARMIDA* NATURAL HISTORY

The subfamily Arsenurinae, constituted entirely of large neotropical saturniids, occurs from tropical Mexico to northern Argentina and contains approximately 57 spp., very few of which are known from the early stages (Lemaire, 1980; Hogue, 1993). However, all 9 species of Arsenurinae occurring in the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (see http://www.acguanacaste.ac.cr; and Janzen, 1988a; 1999) have been reared on-site from wild-caught caterpillars (see Janzen and Hallwachs (2000) for photographs of adults and larvae, and natural history details; and Bernays and Janzen, 1988; Janzen 1982, 1984, 1986, 1987, 1988b, 1993; Janzen and Gauld, 1997).

Arsenura armida occurs in tropical Mexico (from Tamaulipas to Chiapas on the Gulf of Mexico slope, up the Sierra Madre Oriental to mid-elevations) to Bolivia and southeastern Brazil (Lemaire, 1980; M. A. Balcázar Lara, pers. comm.). In the ACG dry forest, its caterpillars have been found feeding on *Guazuma ulmifolia* (Sterculiaceae), *Rollinia membranacea* (Annonaceae), and *Bombacopsis*

quinatum (Bombacaceae); in the ACG rainforest it feeds on *Heliocarpus appendiculatus* (Sterculiaceae) (Janzen and Hallwachs, 2000). Egg masses have also been found on these dry forest food plant species. *Arsenura armida* occurs through lowland Costa Rica (below 500-1000m) in all wildland ecosystems from dry forest to very wet rainforest (label data from specimens in INBio, see http://www. inbio.ac.cr), but has not been reared elsewhere. Hilje *et al.* (1991) list *A. armida* caterpillars as an occasional "pest" of *Guazuma ulmifolia* grown as cattle forage in Central America. The other 8 species of ACG Arsenurinae are non-social and feed cryptically and solitarily on the foliage of the same and other species of large trees (Janzen and Hallwachs, 2000) and will be discussed in detail elsewhere.

The following natural history account is based on the individual rearing and observation records available in Janzen and Hallwachs (2000) and Janzen's personal observations between 1978 and 1999.

In the ACG dry forest, the peak of *Arsenura armida* eclosion occurs between the first and last week of June, approximately 3 weeks after the rains begin. This species, along with *Automeris io* (Fabricius) and *Molippa nibasa* (Maassen & Weyding), is among the last three of the 30 ACG dry forest breeding saturniids to eclose after the long (Dec-May) dry season (Janzen, 1993). It passes the long dry season as a solitary and dormant pupa in a chamber excavated 2-10cm below the soil surface. It cannot be determined whether pupation of a given newly-eclosed June adult occurred at the end of the first generation in the previous Jul-Aug, or at the end of the second generation in the previous Nov-Dec. This is because part of the first generation enters a dormant pupal stage and part ecloses about 35-55 days after pupation, to create a second generation (Nov-Dec). All of the second generation pupae become dormant until the following Apr-May beginning of the rainy season.

In captivity, both sexes eclose about an hour after dark and mating of females takes place that night. The following night, if she finds a suitable food plant (which is the usual case in the ACG dry forest where *Guazuma ulmifolia* and *Bombacopsis quinatum* are common trees), the female usually lays her entire egg load in one mass on the underside of one leaf (Fig. 1-2). Occasionally, however, she splits the clutch into two roughly equal-sized masses, both of which may be laid on the same night or over two nights. The entire egg mass contains 350-500 eggs if the female passed her larval life feeding unrestrained on her food plant in the wild. Actual counts of eggs per mass are 432, 440, 461 (*Bombacopsis quinatum*), 361 (*Guazuma ulmifolia*), and 365 and 171 (*Rollinia membranacea*) (1999 records by Costa and Fitzgerald). The latter egg mass was likely a half egg load. Egg loads from adults from caterpillars reared in captivity range from only a few dozen eggs to nearly full-sized, depending on the quality of the food offered the caterpillar. The female lives 6-8 days after eclosion, just as do other (non-feeding as adult) saturniids in this habitat (D. H. Janzen, pers. obs.), with the result that all but two female *Arsenura armida* arriving at lights in the ACG to date (n = 27) have been 100% egg-free (one contained 203 eggs, likely a half egg load given her very large wing area, and the other was an unmated female that had eclosed at least the night before).

The pattern of clustered oviposition by *Arsenura armida* is strikingly different from that of the other 8 species of Arsenurinae in the ACG (*Arsenura drucei* Schaus, *Arsenura batesii* (R. Felder & Rogenhofer), *Arsenura sylla* (Cramer), *Rhescyntis hippodamia* (Cramer), *Caio championi* (Druce), *Titaea tamerlan* Maassen), *Dysdaemonia boreas* (Cramer), and *Copiopteryx semiramis* (Cramer)), all of which lay 1-5 eggs (usually only 1-2) at an oviposition event and none of which appear to be social as caterpillars. The result of this behavior is that the eggs and highly cryptic caterpillars are scattered through the crowns of their food plant trees and widely spread among individual trees as well. A female of these eight non-social species generally uses 5-7 nights to oviposit her entire egg load. When confined to a large plastic bag, a female of one of these species may lay up to several hundred eggs in a night on the walls of the bag, singly and side by side (Fig. 4), but when free-flying she keeps moving through the foliage as she oviposits (Fig. 3, 5).

The eggs of *Arsenura armida* are white to cream-white and only slightly flattened spheres (Fig. 1), as are the solitarily-laid eggs of two other ACG arsenurines, *Arsenura batesii* and *A. sylla* (e.g., Fig. 5), but the solitary-laid egg of *Arsenura drucei* matches the patterns of the other 5 species of ACG Arsenurinae, which are flattened spheroids with a white, cream or light green equatorial band and green to pink hemispheres (Fig. 3-4). An *Arsenura armida* egg weighs approximately 0.0012 g (e.g., 84-SRNP-170 in Janzen and Hallwachs, 2000) while the solitarily-laid egg of *Arsenura drucei* weighs approximately 0.016 g (e.g., 97-SRNP-236 in Janzen and Hallwachs, 2000). A fully-fed (as caterpillar) female *Arsenura armida* with a full egg load weighs about 70% that of a fully-laden fully-fed female *Arsenura drucei*, while her individual eggs only weigh about one tenth as much as do those of *A. drucei*. *Arsenura drucei* lays one half to one third as many eggs as does *Arsenura armida*, but her much larger eggs are widely scattered through the vegetation.

The eggs of *Arsenura armida* hatch after 12-14 days, roughly twice the duration of saturniine and ceratocampine eggs in this habitat, and about half that of hemileucine eggs in this habitat. The first instar larvae are brightly aposematically ringed yellow and black with red heads (Fig. 6), and remain together feeding side by side in large masses on the leaves (Fig. 6-7). In their 3rd (antepenultimate) instar, they begin to rest diurnally in large conspicuous masses on the lower trunk and (underside of) larger branches (Fig. 8), and continue doing this until leaving the tree as prepupae to solitarily excavate a pupation chamber and pupate in the soil. In striking contrast, larvae of the other 8, solitary, species of ACG Arsenurinae are cryptic in all instars, colored as leaf and branch parts (see photographs in Janzen and Hallwachs, 2000). The aposematism of *A. armida* clearly functions to signal unpalatability. Caterpillars of this species are ignored by monkeys and birds in this forest (D. H. Janzen, pers. obs.). Janzen demonstrated larval toxicity by killing a nestling trogon (*Trogon elegans*) by feed it a single late instar *Arsenura armida* caterpillar, and by making two nestmates very sick by the same treatment. Last instar non-social and cryptic caterpillars of *Titaea tamerlan* and *Caio championi* are, however, frequently fed by parent birds to trogon nestlings in the ACG, and feed on *Bombacopsis quinatum* foliage just as did the *A. armida* caterpillars fed to the nestlings (D. H. Janzen and F. Joyce, pers. comm.).

Fig. 1-6. *Arsenura armida* eggs and larvae, and the arsenurine *Dysdaemonia boreas*: **1)** A newly laid clutch of 440 *Arsenura armida* eggs laid by a single female in one oviposition event. This 2 cm diameter egg mass is the entire egg load from one large healthy female (88-SRNP-285). **2)** The same *Arsenura armida* egg clutch as in Fig. 1 after the larvae have hatched and eaten as much of the egg chorion as they will before moving on to feed on leaves (88-SRNP-285). **3)** Single egg of *Dysdaemonia boreas* (Arsenurinae) laid in nature on the under surface of *Ceiba pentandra* leaf in the crown of an adult tree (95-SRNP-4275). **4)** Multiple eggs of *Dysdaemonia boreas* (Arsenurinae) collected from where they were laid on the walls of plastic bag (82-SRNP-775). **5)** Single egg of *Arsenura batesii* laid in nature on the upper surface of a *Apeiba tibourbou* leaf (93-SRNP-5062). The head of a No. 3 insect pin is to the right for scale. **6)** Group of 1st instar *Arsenura armida* larvae derived from the egg mass in Fig. 1-2, feeding together on *Bombacopsis quinatum* (88-SRNP-285). Each larva is 8-10mm long.


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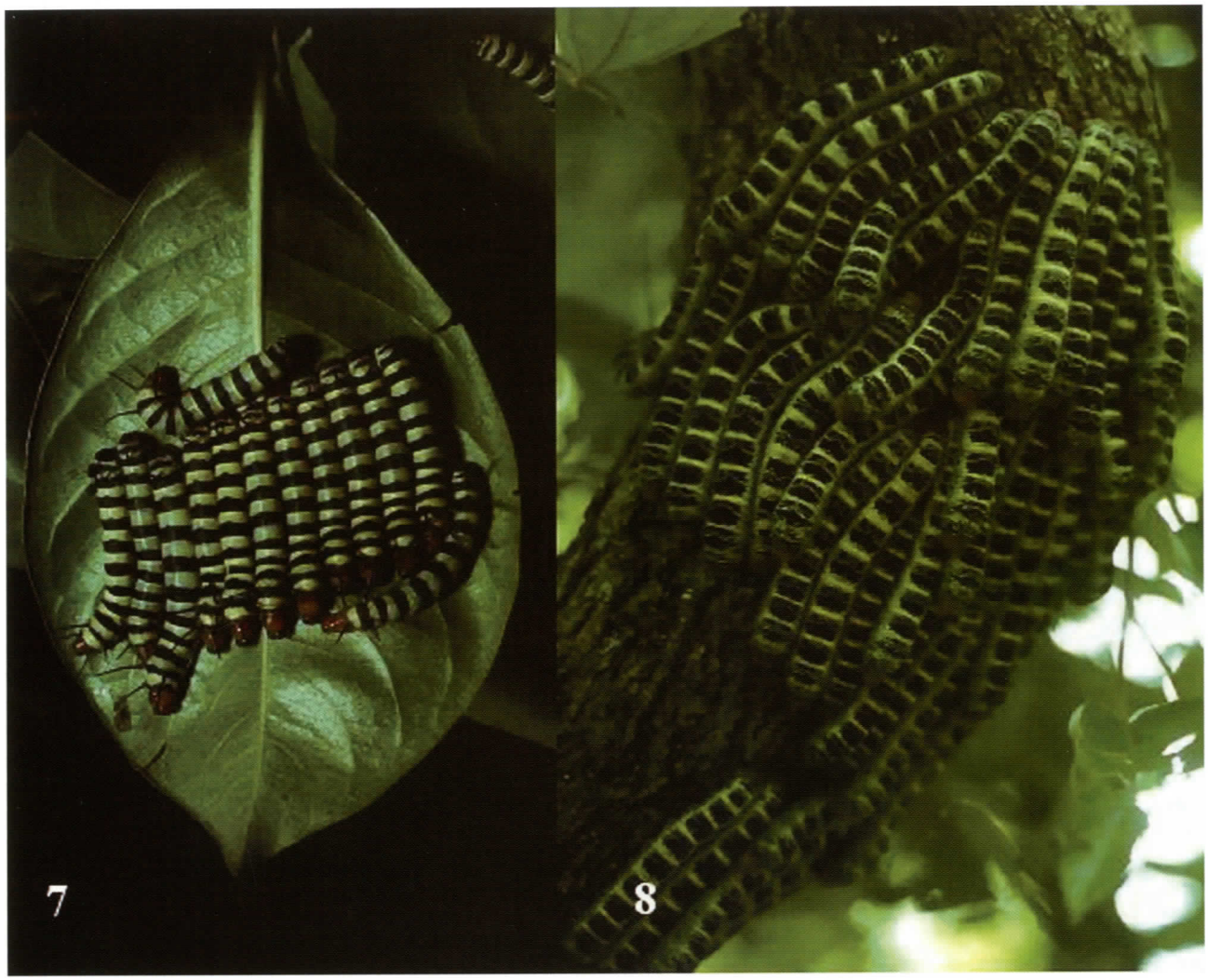

Fig. 7-8. Later instar larvae of *Arsenura armida*: **7)** Group of 3rd instar *Arsenura armida* larvae resting on the underside of a leaf in the crown of a mature *Bombacopsis quinatum* (81-SRNP-822). Each larva is ca. 35mm long. **8)** Group of 5th (last) instar *Arsenura armida* larvae diurnally resting on the lower trunk of *Guazuma ulmifolia* tree (88-SRNP-329). Each larva is ca. 100mm long.

The two "usual" foodplant trees of *Arsenura armida* in the dry forest of Sector Santa Rosa of the ACG have such large crowns that the caterpillars from 1-2 egg masses do not eat enough to cause conspicuous defoliation. However, in the more moist dry forest of Sector Pailas of the ACG, where *Arsenura armida* females appear to prefer to oviposit on the smaller trees of *Rollinia membranacea* (a species that does not occur in the Sector Santa Rosa dry forest), it is commonplace for the caterpillars from a single clutch of eggs to totally defoliate a single food plant.

MATERIALS AND METHODS

Field observations were conducted June 1999 in Sector Pailas of the ACG. The ACG contains 88,000 ha of conserved land area located in northwestern Costa Rica (see http://www.acguanacaste.ac.cr, and Janzen, 1988a,b). Sector Pailas (elev. 500-800m) lies on the interface between the widespread dry-forested lowlands of Provincia Guanacaste and the upper-elevation cloud forests on the Volcan Rincon de la Vieja massif. Observations were made on colonies of *A. armida* feeding on *Rollinia membranacea* (Annonaceae) in the semi-deciduous old secondary dry forest of the Rivas property of this Sector. Salient features of larval feeding and foraging behavior were recorded in the field. Colonies in the 2nd and 4th instar were collected and transported to Estación Biologica Santa Rosa, Sector Santa Rosa, 25 km to the north, for studies of trail-marking behavior. Throughout this paper specific *Arsenura armida* rearing events are cross-referenced with the voucher code for that event as to be found in Janzen and Hallwachs (2000) (e.g., 88-SRNP-285).

We collected surface cuticular residues from the bodies of caterpillars to determine if they elicited trail-following behavior. To collect residues, paper index cards (6 x 8cm) were prepared by trimming to 6 x 6cm and folding along both diagonals to produce four ridges in an X-shape (Fitzgerald, 1998a; Fig. 9). To create artificial trails a 4th-instar caterpillar was grasped between thumb and forefinger and a candidate site was swiped along a ridge 5 times, commencing at the intersection of the ridges at the center of the card and continuing along one ridge for 3 cm. For comparative tests a second candidate site was similarly wiped along an adjacent ridge to form a V-choice. A 2nd-instar caterpillar was then placed at the center of the "X" and its response to the artificial trails recorded. Each test was replicated 10 times with different caterpillars, each time using 4th instars to generate the trails and 2nd instars to test them (this is because the trauma of swiping the very small 2nd instars would confound the experiment by damaging them). A response was considered positive if a caterpillar walked the entire length of the artificial trail without reversing, and time taken to traverse the 3 cm of trail was also recorded. It should be noted that

2nd-instar rather than 4th-instar larvae were regularly used to assay trail attractiveness because group fidelity and reliance on trails often wanes with larval age (Costa and Pierce, 1997); using the youngest available larvae in our trail-following assays thus minimizes the chance of Type II errors.

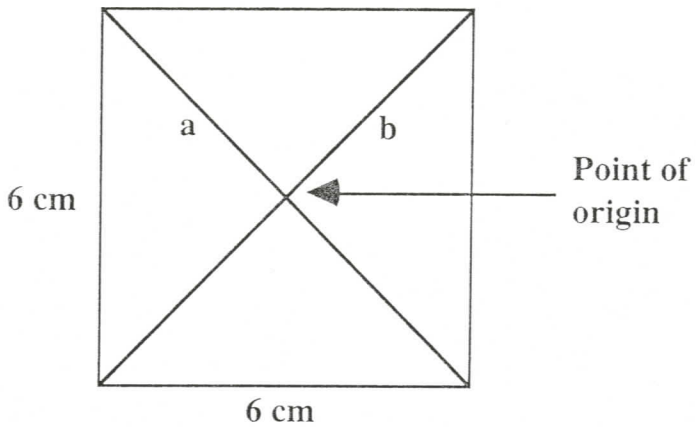

Fig. 9. Schematic diagram of V-maze design used in tests of trail-following in *Arsenura armida*. Arms (a and b) were differentially treated with cuticular material or whole-body extracts derived from 4th instar larvae. Individual 2nd instar larvae were placed at the point of origin and tested for arm choice or time taken to traverse trail, depending on test. See text for details of experimental design and statistical analyses.

In our first V-choice test, caterpillars were allowed to choose between a blank (control) ridge and one treated with residues obtained from the ventral surface of the tip of the abdomen. A second V-choice test was conducted to compare the response of caterpillars to residue obtained from the ventral tip of the abdomen with that obtained from the ventral mid-abdominal region lying between the prolegs. In a final V-choice test caterpillars were presented a choice between cuticular surface wipes taken from the dorsum of the abdomen and a blank (control). The thoracic surface was not tested.

V-choice tests were also conducted to determine how caterpillars responded to solvent extracts of dissected body regions. Two extracts were prepared. For the first, stock extract was prepared by soaking the excised posterior abdominal tips of 20 4th-instar caterpillars in 95% ethanol. Tips were permitted to soak for approximately 1 hour after which they were removed and the solvent concentrated by evaporation to 0.2 ml for testing. Concentrating the extract by evaporation in the high-humidity environment of the ACG field laboratory proved inefficient, so the second extract was prepared by soaking 40 intact 2nd instar caterpillars in more highly volatile acetone for approximately 1 hour and again concentrating the extract by evaporation to 0.5 ml for testing.

In the first set of trail-following assays we observed the response of 2nd instar caterpillars to artificial trails prepared from the first (ethanol) extract. To prepare a trail, 5 ml of the extract was micropipetted along a narrow 3cm line. A 2nd instar caterpillar was placed at the end of the line and its response to the trail recorded. V-choice tests were then conducted to determine if the caterpillars could distinguish between trails differing in strength by a factor of 2. To prepare the artificial trails, 5 ml of the ethanol extract was micropipetted in a 2cm line along one of the diagonal ridges of the V-choice card. Another artificial trail was micropipetted on a second, adjacent ridge prepared from the same extract diluted to 1/2 its original strength with fresh ethanol.

We also conducted a second set of V-choice tests using the identical V-choice procedure described above except that the two trails were prepared with the acetone extract and differed in strength by a factor of 10. Discrimination between trails of different age was also tested with a V-choice assay by laying out an ethanol-extract trail as described above and determining whether caterpillars would choose between it and a new trail of identical concentration laid out 24h later. We also tested caterpillar response to food plant leaf extract and solvents alone as controls; these tests involved micropipetting 5 ml of solvent or leaf extract along a 3cm line.

RESULTS

Groups of 2nd and 4th instar larvae at the study site were found on the leaf undersides on the lowermost branches of relatively young (dbh approx. 9cm) *Rollinia membranacea* trees in insolated sites. Young larvae foraged in typical nomadic fashion, consuming one or more leaves in a patch before moving to a new cluster of leaves. Average migration distance between feeding areas was not recorded, but evidence of 7 distinct feeding areas was found associated with one colony, with feeding areas lying 75-195cm away from the group where we encountered it feeding in one area. Large groups of several hundred larvae, presumably derived from a single egg mass, were fragmented into several loosely associated subgroups on the same tree. The largest group encountered at our study site (n = 70 3rd instar larvae) was broken down into 5 subgroups of 8-24 larvae, with an average distance between subgroups of 28.75cm (as measured along the branches).

Molting larvae aggregate in the center of the leaf underside and spin a small quantity of silk across the surface, apparently to which to anchor the posterior end of the abdomen as an aid to molting. Close observation of the plant surfaces upon which colonies have fed, and handling of living caterpillars, indicated that the larvae spin little or no silk when foraging, feeding, or walking about. It was evident that the larvae were not using silk trails as guides and aggregation mechanisms. Observations of caterpillars under magnification showed that as the caterpillar moves over the plant, the underside of its body, particularly the fleshy area between the anal prolegs, brushes against the surface. On more cylindrical surfaces such as twigs, much of the venter of the abdomen lying between the abdominal prolegs also brushes against the substrate as the caterpillar walks.

In V-choice tests, all 10 larvae selected artificial trails prepared from surface residues of the posterior tip of the abdomen in preference to the blank (control) arm. Surface residues of the dorsum were likewise chosen in preference to the control. Caterpillars also responded to surface residues of the ventral mid-abdominal region, but out of 20 V-choice tests 15 selected trails prepared from tip surface residues over those prepared from mid-abdominal surface residues (chi-square = 5; P = 0.025). We note that the mid-abdominal surface residues could easily have been slightly self-contaminated with residues from the posterior tips of the caterpillars. In all tests, caterpillars proceeded with caution, making apparently careful comparisons between the alternate pathways, by swinging their heads from side to side over the ridges before venturing onto the trail. The caterpillars moved along linear trails with only minimal lateral deviation, suggesting that they use a klinotactic or tropotactic orientation mechanism that makes use of a pheromonal concentration gradient, as previously reported for other trail-following caterpillars (Peterson and Fitzgerald, 1991).

In all of 10 tests, caterpillars traveled the length of the trail at an average velocity of 12.8 +/- 1.46 SE cm/s while following extracts prepared from the ventral surface of the posterior tip of the abdomen. This speed of travel did not differ significantly from that of caterpillars following tip-extract trails (10.7 +/- 1.12 SE cm/s) as described above (1-way ANOVA; F = 1.27, P = 0.274). In 20 replicates of tests to determine the response of caterpillars to trail

strength, 15 larvae selected the stronger of two trails that differed by a factor of 2 (chi-square = 5, P = 0.025), and 19 larvae selected the stronger of two trails that differed by a factor of 10 (chi-square = 16.2, P = <0.0001). The trail longevity assay showed that trails 24h old are competitive with fresh trails: 6 of 15 caterpillars tested selectde the aged trail in two-choice assays, while 9 of 15 selected the more recent trail (chi-square = 0.6, P = 0.44). Caterpillars showed no response to trails prepared either from leaf extracts or solvents alone.

DISCUSSION

Our study indicates that *A. armida* caterpillars passively or actively mark the food plant substrate they are traversing with a pheromone that is associated with the cuticle of the ventral surface of the abdomen. The caterpillars also followed trails prepared with residue obtained from the cuticular surface of the dorsal abdomen. This suggests that the trail pheromone is a general chemical component of the cuticle and is broadly distributed over the surface of the insect's body. However, we cannot eliminate the possibility that the chemical or chemicals involved originate at some glandular orifice, and are somehow spread over the remainder of the caterpillar body. Whatever the case, this is the first caterpillar encountered that appears to mark trails with such a general body odor chemical rather than with a chemical associated with silk or restricted to a specific region of the body. While the silk of some social Lepidoptera has been shown to elicit trail-following by itself, it appears that more commonly an extra-silk chemical pheromone is sufficient to elicit trail following, with the silk playing little or no role (Fitzgerald, 1995). *A. armida* is unique among social Lepidoptera studied to date in that silk is not produced at all when foraging, though this likely reflects the fact that few social Lepidoptera have as yet been closely studied.

Field observations indicate that the pheromone enables the caterpillars to deposit trails as they move to distant feeding sites. These trails presumably facilitate the reaggregation of the group at the new food find, help avoid getting separated from the cohort, and may be used for repeat visits from diurnal resting sites (especially last instar larvae). We cannot determine if this behavior is actively selected for by the depositor of the chemical (because it is useful to have conspecifics in the vicinity, or because of inclusive fitness considerations), by the sensor of the chemical (because it is useful to aggregate with conspecifics), or both. This capability may be particularly important in later instars (especially 5th) when caterpillars rest at a repeatedly-used site on the lower trunk of the tree in the day (Fig. 8) and forage at sites many meters distant from this site during the night.

The ability to distinguish trail strength also may be used by the caterpillars to take the pathway marked by the largest number of individuals, leading to the whole group aggregating at a particular site. However, the fragmentation of a group into several subgroups as observed in this study is also consistent with the use of a chemical trail marker and sensitivity to marker-strength (Fitzgerald and Costa, 1986). Local choice point decisions by small groups may be proximately influenced by recent choices by conspecifics.

The conspicuously aposematic *A. armida* caterpillars both rest and forage in the open, rather than resting in a communal shelter as do many other social caterpillars. Their nomadic behavior within the food plant crown is commonly observed among other aposematically colored social caterpillars (Fitzgerald, 1993a; Costa and Pierce, 1997). As the caterpillar grows in size, it shifts from resting on the leaves (Fig. 7) to resting on the trunk of the food plant (Fig. 8), presumably because the latter provides a large contiguous surface that can accommodate a tightly packed aggregation of up to hundreds of large (10-20 g) caterpillars. A similar shift occurs with the forest tent caterpillar *Malacosoma disstria* (Hübner) (Fitzgerald and Costa, 1986; Fitzgerald, 1995). It is also possible that the late instar caterpillars are better able to avoid oviposition by their tachinid and ichneumonid parasitoids (e.g., *Winthemia subpicea* (Walker) and *Barylypa broweri* Gauld, Janzen and Hallwachs, 2000) when grouped on a flat tree bark surface than they would be if draped in the twigs and leaves overhead with more exposed body surface area. The smaller earlier instars can achieve the same tight packing and ventral protection simply on leaf surfaces.

It is unknown if the great longevity of the trail demonstrated under laboratory conditions applies equally to field conditions; long pheromone-based trail life is typically associated with organisms that repeatedly use the same pathways to and from resting sites. *Arsenura armida* does do this in the 4th and especially 5th-instars when the caterpillars move nocturnally between a resting site on the lower trunk (Fig. 8) and distant feeding sites in the crown above.

Arsenura armida is the only known Neotropical arsenurine to exhibit a combination of strong aposematism, gregariousness and trail-following behavior, although it is possible that larvae of at least some members of the closely related complex of *Arsenura* species comprising *A. armida*, *A. archianassa* Draudt, *A. mossi* Jordan, *A. ciocolatina* Draudt, *A. beebei* (Fleming), *A. delormei* Bouvier, *A. albopicta* Jordan, *A. polyodonta* (Jordan), and possibly *A. rebeli* (Gschwandner) (Lemaire, 1980) exhibit all three traits as well. Regardless of whether this suite of characters is restricted to *A. armida* or to the *A. armida* complex, it probably has a single evolutionary origin. Seen in the broader context of the sizable genus *Arsenura* and the subfamily Arsenurinae, this raises interesting questions concerning the evolution of these traits. Sillén-Tullberg (1988, 1993) concluded from her phylogenetic analysis of gregariousness and aposematism in butterfly larvae that aposematism often evolutionarily precedes gregariousness. In this view, aposematism in solitary larvae is seen as a predisposing factor for social evolution, probably favoring grouping (selection for attendant chemical signals that facilitate grouping) through group-enhancement of warning signals (reviewed in Costa and Pierce, 1997). The Arsenurinae, however, exhibit little interspecific variation in these traits: of approximately 23 *Arsenura* species, only *A. armida* is known to be aposematic and social (D. H. Janzen, pers. obs.), suggesting that sociality may have independently arisen in this species rather than sharing a common phylogenetic origin with other social saturniids. This idea is supported by Peigler's (1993) cladistic treatment of arsenurine genera, which suggests *Arsenura* and allied genera (*Caio*, *Dysdaemonia*, *Paradaemonia*, and *Titaea*) are not basal in this subfamily.

It is not known if any of the solitary arsenurine caterpillars exhibit central place foraging, reusing the same resting site after successive foraging trips. In all cases known in the ACG, the solitary species perch on the undersides of leaves in the first three instars, and on stems and branches in the last two instars. Trail-marking behavior is found in some solitary lepidopteran larvae, including those of the papilionid *Iphiclides podalirius* (Linnaeus) (Weyh and Maschwitz, 1982) and the charaxine butterfly *Polyura pyrrhus* (Linnaeus) (Tsubaki and Kitching, 1986). Caterpillars in these species appear to mark individual trails that enable the larvae to relocate their resting sites, typically located some distance from their feeding sites. Costa and Pierce (1997) speculate that this solitary foraging strategy may represent an ancestral context for the evolution of trail-marking behavior. This may have then in turn become elaborated in a group or social context, shifting its function to promote group cohesion and in some lineages being employed in recruitment communication (e.g., some tent caterpillars; Fitzgerald,

1995).

These ideas suggest two promising avenues for further inquiry into the evolution of sociality in *Arsenura armida*. First, phylogenetic approaches could be used to reconstruct the *A. armida* social-evolutionary pathway. Resolving phylogenetic relationships of *Arsenura* species would shed light on the placement of *A. armida* with respect to other aposematic *Arsenura*, providing an interesting test of Sillén-Tullberg's (1988) hypothesis of aposematism predisposing the evolution of gregariousness in larval Lepidoptera, while a phylogenetic treatment of Neotropical saturniid subfamilies known to contain social species would help establish the likely number of independent origins of sociality in this family. Second, an investigation of individual trail-marking and central-place foraging in solitary congeners of *A. armida* could help identify the range of uses of the trail pheromone; trail-marking by solitary species may suggest an ancestral context for social trail-marking in *A. armida*. In addition, the work reported here raises a host of questions concerning proximate mechanisms of trail-marking in this species. Further study is required to determine if the *A. armida* trail pheromone is a generalized cuticular compound. Cuticular hydrocarbons, for example, are well-known to function pheromonally in social Hymenoptera (Ross and Matthews, 1991), and are logical candidates for trail markers.

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