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LATE-INSTAR SHIFT IN FORAGING STRATEGY AND TRAIL PHEROMONE USE BY CATERPILLARS OF THE NEOTROPICAL MOTH *ARSENURA ARMIDA* (CRAMER) (SATURNIIDAE: ARSENURINAE)

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ABSTRACT. Caterpillars of *Arsenura armida* (Cramer) (Saturniidae: Arsenurinae) are diurnal nomadic foragers in early instars, maintaining aggregations within the host tree crown through the use of a trail pheromone. In the fourth instar, larvae switch foraging strategies to become nocturnal central place foragers. In central place foraging mode, the caterpillars rest by day on the trunk of the food plant, ascend to the canopy at nightfall to feed, and then return to the lower trunk by dawn, often at the same resting (bivouac) sites as used previously. Peak activity ascending to and descending from the canopy occurs in twilight. Central place foraging *A. armida* caterpillars do not maintain colony structure at night, but disperse in the canopy to feed singly. The caterpillars appear to use tree architecture and their trail pheromone to relocate conspecifics (which are generally confamilials) upon descending. While bivouac sites are often reused, individual caterpillars do not exhibit strict site fidelity and may go to a bivouac site different from whence they came. This shift in foraging behavior entails a concomitant change in reaction to the information content of *A. armida*'s trail pheromone, from maintaining groups as the caterpillars move from patch to patch, to relocating distant resting sites. Diurnal resting bivouacs are probably warning displays, and we discuss this behavior in the context of *A. armida*'s defensive ecology.

Additional key words: trail-following, group foraging, social caterpillars, chemical communication, tropical dry forest.

Larval sociality is widespread in the Lepidoptera, occurring in an estimated 27 families in 19 superfamilies (Costa & Pierce 1997). Expressions of sociality in this order vary considerably, and may include group defense, group nest or shelter construction, and/or group foraging (e.g., Fitzgerald 1993a, Costa & Pierce 1997). Fitzgerald and Peterson (1988) suggested that communication complexity of caterpillar societies can be categorized by foraging strategy, identifying three basic modes of group foraging (patch-restricted, nomadic, and central place foraging) that in part reflect the extent of communication and cooperation by group members. Patch-restricted foragers remain more or less in a single patch or feeding site for the duration of the larval stage, typically constructing nests by tying leaves with silk or wholly enveloping leaves in masses of silk and extending the bounds of the nest as food becomes locally exhausted (e.g., the ugly nest caterpillar *Archips cerasivoranus* (Fitch), Tortricidae). Nomadic foragers, in contrast, move en masse among patches, constructing no shelters and often exhibiting aposematic coloration (e.g., notodontids like *Anisota* or *Datana* spp.). Finally, central place foragers nest or rest in a fixed location, periodically leaving the site to feed; for example the eastern tent caterpillar *Malacosoma americanum* Fab. (Lasiocampidae) and the madrone caterpillar *Eucheira socialis* Westwood (Pieridae) (see additional examples in Fitzgerald 1993a, Costa & Pierce 1997).

Although the behavior of relatively few social Lepidoptera have been studied to date, species representing each of these foraging strategies have been shown to communicate via trail pheromones. *A. cerasivoranus*, for example, uses a pheromone to promote within-patch aggregation (Fitzgerald 1993b). Fitzgerald and Costa (1986) studied the nomadic foraging lasiocampid *Malacosoma disstria* Hübner, the forest tent caterpillar, which also uses a trail marker for group cohesion. Its congener, the central place foraging *M. americanum*, is the only social caterpillar thus far shown to engage in elective recruitment to food. This species employs a two-part trail system consisting of exploratory and recruitment trails used to direct tentmates to high quality food patches (Fitzgerald & Peterson 1983).

The foraging strategy of some social caterpillars is intermediate between the three basic strategies delineated by Fitzgerald and Peterson (1988), and some species switch strategies as they grow. It is very common among social Lepidoptera and Symphyta for group fidelity to wane over time such that the penultimate or ultimate instars forage solitarily, and many begin their lives feeding as a group at the site of larval eclosion through at least the first instar, but soon shift to nomadic or central place foraging. These cases might represent, respectively, the beginning of the dispersal phase or delayed commencement of active foraging, and so may not be good examples of strategy

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switching per se. Only a few species are known to exhibit behavioral changes in later instars, but the list is growing. For example, in the penultimate or ultimate instar the arctiid *Hyphantria cunea* Drury switches to central place foraging, as does the European pine processionary *Thaumetopoea processionea* (Linnaeus) (Notodontidae) (T. D. Fitzgerald pers. obs.). The saturniids *Hylesia lineata* Druce and *Automeris zugana* Druce feed diurnally as a group of sibs in nomadic fashion through the second instar, when they commence nest building and switch to nocturnal central place foraging (DHJ pers. obs.). Insofar as shifts in foraging strategy by social caterpillars reflect an evolved response to temporal changes in host quality or predation pressure, and are likely to be accompanied by shifts in communication mode, these species may be informative model systems with which to study factors shaping caterpillar social behavior.

Few studies to date have focused on developmental shifts in social caterpillar foraging strategy, and no social caterpillar has yet been shown to use a trail marker for different uses over time (though this is likely to be common). Here we report a change in foraging strategy and trail marker use by larvae of the Neotropical arsenurine saturniid *Arsenura armida* (Cramer) in northwestern Costa Rica. Costa et al. (2003) showed that the aposematic early instars of *A. armida* forage nomadically and use a trail pheromone to promote grouping. One of us (DHJ) previously observed that this species switches its foraging behavior in later instars, becoming a central place forager in that the larvae form sizable groups on the trunk of their host tree, leaving these sites to forage at night and reassembling at dawn or earlier. The present study documents this foraging mode by late instar *A. armida* with observational and experimental data. In particular, we address the following questions: (1) Do *A. armida* larvae continue to forage socially (in groups) in late instars? (2) Do larvae exhibit fidelity to a resting site, returning daily to the same location on the host tree? And (3) if group foraging and/or reusing resting sites, how might larvae use their trail marker to do so?

Arsenura armida belongs to subfamily Arsenurinae, consisting of approximately 57 species of Neotropical saturniids found from tropical Mexico to northern Argentina (Lemaire 1980, Hogue 1993). This species occurs from tropical Mexico to Bolivia and southeastern Brazil (Lemaire 1980, Balcázar & Beutelspacher 2000), and is found throughout lowland Costa Rica from dry forest to rainforest (for label data from specimens in INBio, see http://www.inbio.ac.cr). In the tropical dry forest of northwestern Costa Rica, ovipositional hosts include guacimo (*Guazuma ulmifolia* Lam., Sterculiaceae), on which it is an occasional pest (Hilje et al. 1991), *Rollinia membranacea* Triana & Planch (Annonaceae), and pochote (*Bombacopsis quinatum* (Jacq.), Bombacaceae) (Janzen & Hallwachs 2003).

The following life history overview is based on rearing and observation records available in Janzen and Hallwachs (2003) and Janzen's personal observations between 1978 and 2000. A more detailed overview with photographs is provided in Costa et al. (2003). The peak of *A. armida* adult eclosion occurs between the first and last week of June in the Area de Conservación Guanacaste (ACG) dry forest, approximately three weeks after the rains begin (Janzen 1993), having passed the dry season as a solitary pupa in a chamber excavated in the soil. Part of the first generation enters dormancy as pupae and part ecloses about 5–8 weeks after pupation to create a second generation (November-December). All of the second generation pupae become dormant until the start of the following rainy season. After mating, female *A. armida* usually lay their entire egg load (350–500 eggs) in a single mass on the underside of a leaf, although split clutches are sometimes observed. The eggs hatch after about 2 weeks and the larvae remain brightly aposematic through their first three instars. Colonies of young instars forage nomadically using trail pheromones to promote colony cohesiveness, and silk plays no role in trail following (Costa et al. 2003). In the fourth (penultimate) instar, the larvae switch their foraging strategy and begin to rest diurnally in large bivouacs on the lower trunk and underside of larger branches. Larvae remain together in this manner until late in the terminal stadium, when they abandon the tree as prepupae.

MATERIALS AND METHODS

Insect collection. One hundred twenty five penultimate (fourth) instar *A. armida* caterpillars, 4–5 cm in length, were collected from a large (ca. 15 m tall) *B. quinatum* tree in the Cafetal area of Sector Santa Rosa, ACG, Guanacaste Province, Costa Rica. At least two large aggregations were found on this tree, each consisting of >200 larvae, with smaller groups nearby. Based on an average clutch size of about 450 eggs (Costa et al. 2003, Janzen & Hallwachs 2003), these aggregations may represent one or two family groups that have fragmented. Approximately half the individuals of an accessible lower aggregation were collected, leaving one large upper group and approximately half the second lower group (collectively numbering three to four hundred larvae) on the tree for later field observations. The larvae were transported to the research center at the Administration Area of the ACG,

where they were divided into three groups, each of which was transplanted onto a young host tree so they would be accessible for observation and experimentation. One group was transplanted onto a 5 m tall *B. quinatum* sapling and two groups were transplanted onto adults of an alternate host, *Guazuma ulmifolia.*

The first transplant tree (G1) was a *G. ulmifolia*, ca. 4 m in height and split into two main trunks about 30 cm above the base, DBH = 17 cm and 18 cm, respectively. A bag containing 40 larvae on *G. ulmifolia* foliage was attached to the lower trunk of the tree, and the larvae were permitted to exit the bag ad libitum. Within two hours nearly half of the caterpillars had exited and formed a group on the trunk about 40 cm above the ground, and within 24 h, 37 were accounted for, occurring singly or in one of several groups or bivouacs. Each individual was then given a bivouac-specific mark on the dorsum of the anal segment (anal plate) or on one or both anal prolegs using a fine tip Sharpie® marker, after observations of test larvae showed that marking did not have an adverse effect. Singletons were also identified with a unique mark, and bivouac sites were marked with labeled pins to test for bivouac fidelity.

The second *G. ulmifolia* (G2) was ca. 2 m in height, DBH = 4 cm, small enough to document the position of each larva in the canopy. Prior to release, 15 caterpillars were marked on the anal plate using white Liquid Paper® correction fluid and given a unique number with a fine-tip Sharpie® marker. Prior to release on the tree, larvae were observed for a 24 h period following marking to ascertain they were not adversely affected by the marking procedure. There was no mortality and all larvae seemed to feed normally. Larvae were transplanted onto the tree using the same method as for G1. At the end of the first day, eleven of the larvae were relocated. Finally, the *B. quinatum* (G3) was about 5 m in height, DBH = 16 cm. Forty larvae were permitted to move onto the new host in the same manner as the transplanted G1 caterpillars. Observational and experimental data were collected from these groups over a 10 day period and used to address (1) larval foraging periodicity, (2) mode of larval foraging (i.e., group vs. solitary foraging) day and night, and (3) the use of trail markers in foraging and bivouac formation.

Group foraging. The group foraging dynamics of *A. armida* was assessed in three interrelated sets of observations. First, mobilization of the caterpillars from their daytime resting bivouacs to nocturnal foraging mode, and their subsequent return and reassembly into bivouacs at dawn, was observed for seven consecutive days. Bivouac fidelity and group composition was documented by noting the position of marked G2 larvae each morning after all larvae had returned and selected a resting site. Because resting groups can be loose, often broken into two or more closely situated subgroups, initial bivouac sites were arbitrarily defined as a roughly circular area 15 cm in diameter centered on resting groups. Any larvae subsequently found within that area were scored as resting at that bivouac. Each bivouac site, including any new sites, was checked daily between 10:00 and 11:00 h for presence of larvae, and each larva's bivouac of origin was noted daily. In addition, the canopies of each tree were searched to account for larvae that had not returned to a bivouac by the daily census time.

The location of each larva of the G2 colony was documented in pre-dawn counts prior to the return of the larvae from the canopy on two separate days. Counts were made with brief use of indirect lighting so as to minimize disturbance to the larvae. To determine if colonies mobilize and depart from their bivouac en masse more rapidly than they recoalesce at dawn, we timed the rate of departure from and arrival to bivouac sites for all three experimental groups. Finally, we observed mobilization of two naturally-occurring field colonies at dusk to ensure the behavior we observed in the manipulated groups was consistent with larval behavior on larger food plants.

Late-instar trail following. To supplement observations of putative trail-following behavior, we prepared a pheromone extract with hexanes. Five 4th-instar larvae were soaked whole in 10 ml pure hexanes for 24 h. Larvae were then removed and the hexane extract concentrated by evaporation to 2 ml. Extract activity was tested using a Y-maze procedure with young 3rd-instar *A. armida* (Costa et al. 2003). 50 µl of extract was micropipetted onto the stem and one arm of a Y-maze on an index card, each of which was 4 cm in length; the same quantity of pure hexane was micropipetted onto the alternate arm as a control. Test larvae were allowed to walk up the main stem of the Y-maze and choose an arm in each of 10 trials, each of which used a fresh Y-maze and a new test larva. Larval choices were statistically evaluated using a Chi-square test corrected for continuity (Zar 1999).

Costa et al. (2003) suggested the cuticle of *A. armida* may be impregnated or coated with a trail pheromone, based on the observation that cuticular wipes from the dorsum and venter elicited trail following. At the end of one week the experimental groups in the present study molted to the final instar, affording an opportunity to test for activity of hexane extracts of the exuviae. Fresh exuviae of 20 caterpillars were collected and soaked in about 2 ml hexane for 36 h. We

tested the extract for trail-following activity using the method described above using early 3rd instar *A. armida* (15 replicates), and analyzed arm choice data with a Chi-square test as above.

Testing if late instar larvae employ trail pheromones when foraging proved difficult, as late instars become agitated when handled. To get around this problem we conducted the following in situ trail-following experiment: we presented randomly chosen larvae walking ad libitum on their host tree during their mobilization or reaggregation periods at dusk or dawn, respectively, with either 50 μl of pheromone extract or 50 μl of pure hexane, applied by micropipette directly to the tree surface at an approximate 45° angle leading away from the larva's direction of movement. The response of each larva was scored as positive (stopping to sweep and investigate the trail and/or deviating to follow the trail) or negative (no discernable response). We conducted a total of 28 trials over two days (18 treatments and 10 controls), and statistically evaluated responses as a 2 × 2 contingency table using Fisher's Exact Test (Zar 1999).

RESULTS

Group foraging and bivouac use. The groups transplanted on *G. ulmifolia* and *B. quinatum* readily assembled into one or more diurnal bivouac. After 24 h a total of 36 of the 40 G1 larvae were recovered; these established 5 initial bivouacs with 3, 9, 6, 7, and 5 larvae, respectively, plus 6 singleton larvae. All 11 G2 larvae were recovered after 24 h, in a single bivouac, but only 22 of 40 initial G3 larvae were recovered after this period, and these occurred in two closely situated bivouacs near the base of the trunk. Many of the larvae not recovered after this initial 24 h period were subsequently observed to join bivouacs, indicating that they had been undetected, probably in the canopy, and had not left the food plant or succumbed to predation. Daily observations of groups on all three trees revealed that larvae remain largely quiescent during the day and do nearly all of their foraging at night. A variable number of larvae were found bivouacked each day, ranging from all to about half of accountable larvae in a given colony (G1: 94–53%, G2: 100%, G3: 81–67%; Table 1). Most of the remainder were relocated resting as singletons or in pairs. In addition, we found that diurnal quiescence may be punctuated with brief periods of activity in which larvae either change resting position or temporarily ascend the trunk to feed. In several cases larvae that became active were observed to return to a resting site within about 30 min, but often not the same site from which they departed. These mid-day movement events are evident in a comparison of bivouac censuses taken in the morning and afternoon for colony G1 (Table 2), showing low levels of diurnal larval movement both between different bivouacs and between bivouacs and the canopy over four consecutive days.

TABLE 1. Proportion of *Arsenura armida* caterpillars in study groups occurring in diurnal bivouacs.

Day of observation	Total number of larvae observed	Number of larvae in a bivouac (%)
A. G1 on *Guazuma ulmifolia*		
1	35	33 (94)
2	32	29 (91)
3	32	17 (53)
4	24	18 (75)
5	27	14 (52)
6	23	13 (56)
B. G2 on *Guazuma ulmifolia*		
1	11	11 (100)
2	11	11 (100)
3	11	11 (100)
4	11	11 (100)
5	11	11 (100)
C. G3 on *Bombacopsis quinatum*		
1	23	18 (78)
2	23	18 (78)
3	16	13 (81)
4	16	13 (81)
5	15	10 (67)

On a daily basis we found that most resting larvae occurred in a group, but we consistently observed a subset of caterpillars that rested apart from conspecifics as singletons or doubletons on the host trunk, under a branch, or on foliage. These caterpillars would cycle in and out of groups seemingly at random. For example, we marked with correction fluid four singleton caterpillars found in the G3 tree canopy, and on four successive days of observation found one, two, or none of these caterpillars had joined the group in the bivouac at the base of the trunk. Similarly, in several instances certain marked G1 and G3 individuals would disappear (presumably remaining high in the canopy where they were missed in our searches), reappearing after one or more days either solitarily or with a group. The number of caterpillars in bivouacs accordingly fluctuates from day to day in our study due to this semi-independence of larvae (see below).

As darkness falls, all larvae ascend to the canopy to feed. Grouped larvae do not depart their bivouacs simultaneously, but mobilize over a period of up to two hours. The first larvae can become active as early as an hour or more prior to sunset, departing their group and ascending to the canopy. Most, however, mobilize during twilight. In one week of observations we found that most larvae ascend by the end of astronomical twilight (approx. 18:30 h local time through the first half of July at the ACG), with peak departure occurring during twilight (Fig. 1A). As twilight progresses larvae become in-

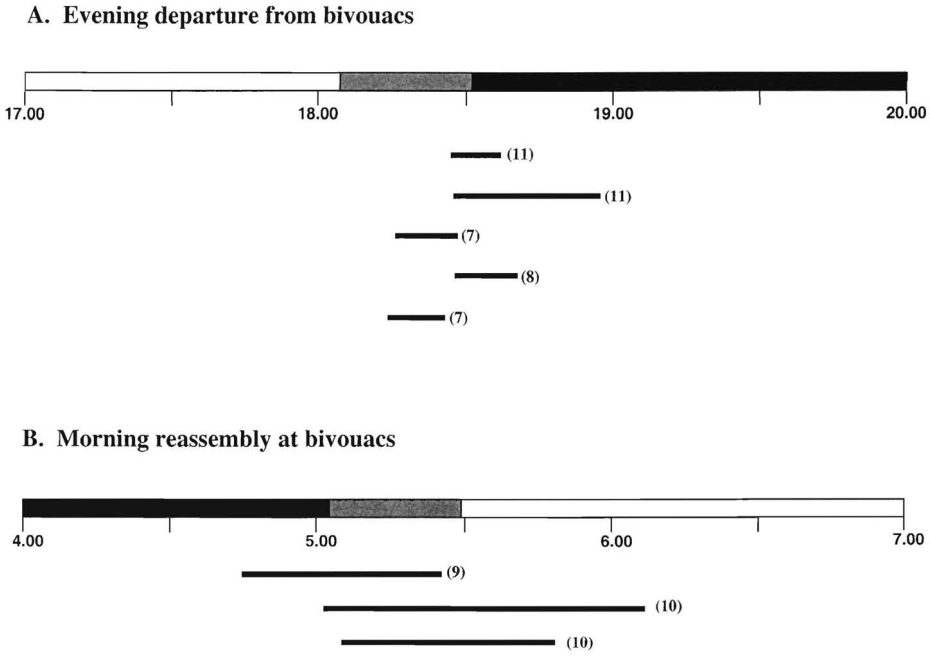

FIG. 1. Periods of daily departure from **(A)** and reassembly at **(B)** diurnal bivouacs for 5 and 3 groups of larvae, respectively. Each bar corresponds to a single group of caterpillars at one bivouac site (number of larvae initially or ultimately occupying each bivouac is given in parentheses), and begins with the departure or arrival of the first caterpillar and ends with the departure or arrival of the last caterpillar at that bivouac. Shading in each graph denotes solar position: stippled = astronomical twilight, black = night, open = day. Observations were made 16–19 July, but times of sunrise and sunset change only slightly from day to day in circumsolsticial weeks. Note that larvae departing bivouacs in the evening become mobilized largely toward the end of twilight, but must begin to leave the canopy prior to morning twilight in order to have been observed arriving to bivouacs during twilight. The time taken to return to bivouacs in the morning is far longer than that of departing bivouacs in the evening, presumably because the larvae are returning from widely varying distances in the canopy.

creasingly active, and small columns indicative of trail following were often observed when pairs or small groups of larvae chanced to become active at the same time. Night observations of feeding and resting G1 and G2 caterpillars revealed that the caterpillars do not forage in groups in the canopy. The small size of the G2 host tree made it possible to map the position of each larva, and in three pre-dawn position plots all caterpillars were observed actively feeding or resting solitarily. This was consistent with positional plots of larvae we could relocate on the other trees: larvae appear to feed and rest individually in the canopy at night and less frequently in loosely associated pairs or small groups.

Each morning the foraging caterpillars returned from the canopy and reassembled into bivouacs. Reassembly also takes place largely during twilight, and takes considerably longer than the evening departure (Fig. 1B). Our data reveal a stochastic element to larval reassembly despite evidence for trail following (discussed below): some bivouac sites were reused on several consecutive days, while others were abandoned after a single use (Table 2). Nonetheless, in our study larvae were more likely to reassemble at bivouac sites used the previous day (recently occupied bivouacs were reused in 20 of 29 bivouac reassembly observations of groups G1 and G3; $\chi^2 = 4.17$, $p = 0.041$). Significantly, although bivouac sites were often reused (Table 3), individual larvae did not exhibit consistent bivouac fidelity, but often regrouped each morning with at least some different conspecifics (Fig. 2).

TABLE 2. Representative daytime movement observations of bivouacked *Arsenura armida* caterpillars over 4 consecutive days of observation.

	10 July		11 July		12 July		13 July	
Bivouac[1]	AM[2]	PM	AM	PM	AM	PM	AM	PM
B	0	0	7	7	2	2	**9**	**7**
C	19	19[3]	0	0	0	0	0	0
D	8	8	**7**	**6**	**9**	**3**	3	3
E	**1**	**0**	**8**	**8**[4]	0	0	**3**	**2**
F	6	6	0	0	0	0	0	0
G	n/a		7	7	8	8	0	0
H	n/a		n/a		n/a		**3**	**0**

[1] Subset of total bivouac sites tracked (see Table 3).

[2] Number of caterpillars observed at each bivouac was noted at approximately 10:00 and 14:00 h Local Time each day; instances of change in larval makeup between AM and PM observations are noted in bold. n/a indicates bivouac was not yet established.

[3] Some change in larval position within bivouac.

[4] One larva departed and one joined.

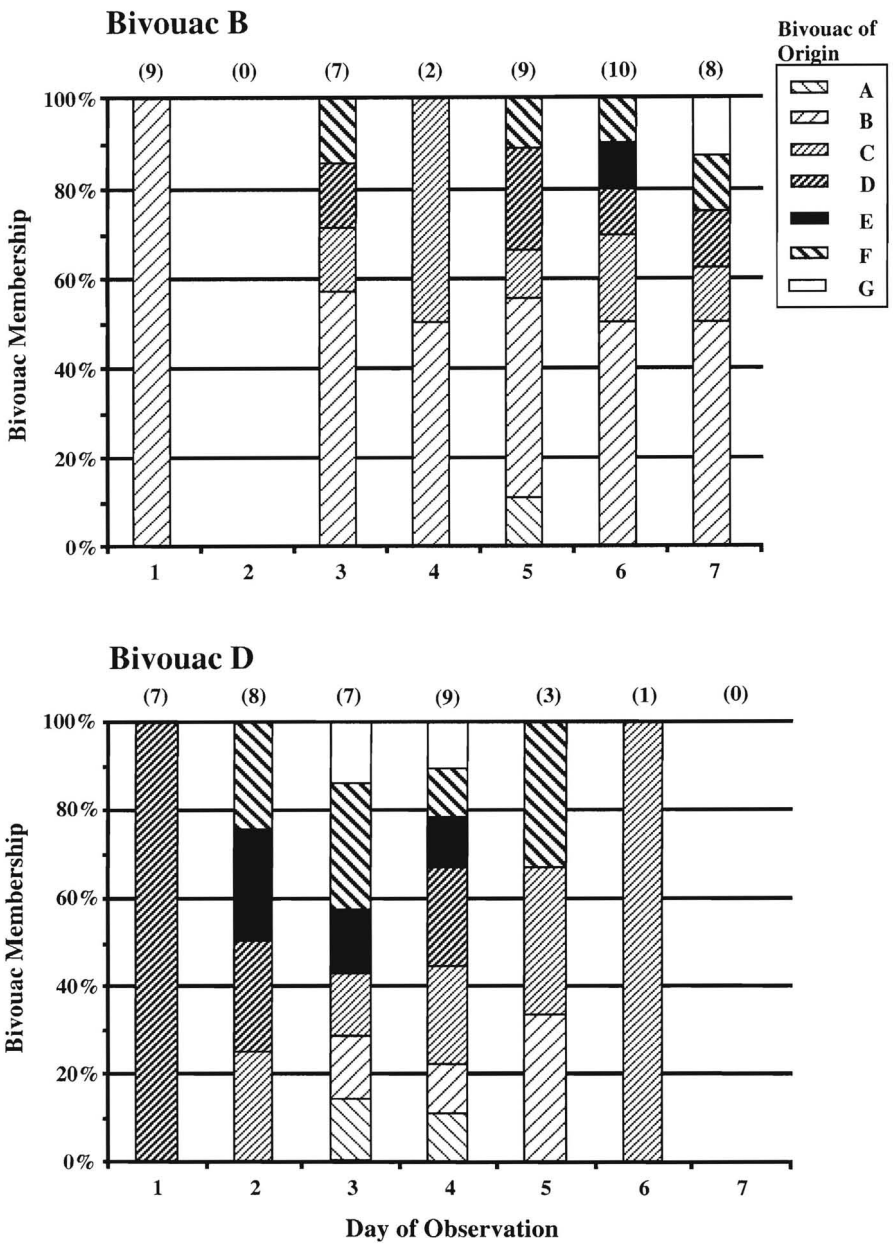

FIG. 2. Daily composition record for two representative bivouac sites monitored on one tree. All larvae were initially (Day 1) given bivouac-specific markers and the bivouac position was marked with a pin (see methods for details). Note that the subsequent number of caterpillars and their initial bivouac of origin vary greatly over successive days, though bivouac B illustrates repeated reuse by many of the same larvae.

Trail following by late-instar foragers. The tendency for bivouac sites to be attractive to larvae on successive days does not necessitate being relocated pheromonally, but our observational and experimental data confirm that trail markers are used by *A. armida* when moving between resting and feeding sites. Y-maze bioassays of cuticular hexane extracts made from late instars proved attractive to early instars ($\chi^2 = 6.4$; $p = 0.011$), and in situ tests of pheromone extracts indicated that late instars find the cuticular extracts attractive: test larvae responded positively in 16 of 18 treatment (hexane extract) in situ tests, but showed no response in 7 of 10 control (pure hexane) tests, a highly significant result (Fisher's Exact Test, $p = 0.0028$). Further evidence supporting the idea that the pheromone is in or on the cuticle is provided by the exuvium extract bioassay results, in which test larvae selected the exuvium extract-treated Y-maze arm in 13 of 15 trials ($\chi^2 = 8.07$; $p = 0.005$).

DISCUSSION

Arsenura armida is one of a few social Lepidoptera or Symphyta known to exhibit a late-instar shift in foraging strategy. Through the 3rd instar *A. armida* larvae forage as nomadic groups, feeding and resting on the leaves of the food plant at each patch. Our observations and experimental data confirm that this species switches to central place foraging in the 4th (penultimate) instar. In switching from nomadic to central place foraging, *A. armida* also shifts the manner in which its trail pheromone is used. As nomads, the trail pheromone is likely used to promote group cohesion, and as such would be used to mark trails between feeding sites. As central place foragers, in contrast, the pheromone conveys information for relocation of a previously-occupied site (or at least return to the vicinity of that site) when forming dawn bivouacs.

The dawn reaggregation dynamic has an element of stochasticity stemming from several sources. First, reaggregation is influenced by tree shape. Trees with a single trunk funnel or channel scattered nocturnally foraging larvae to a common location more readily than do trees divided low into multiple trunks (*G. ulmifolia* often exhibits a coppice-like multi-trunked growth form in the ACG, while *B. quinatum* does not). We are confident that the caterpillars do not rely on tree architecture alone to assemble into bivouacs, however, since they often make directed, non-random movements to previously-used sites, many of which are reached following a circuitous path around the trunk. We are also confident that silk plays no role in relocation: as previously documented for early instars, late instar *A. armida* produce no silk when walking. Larvae use their pheromone to relocate the vicinity of the bivouac at which they rested the day before, but often end up resting at alternative sites.

It is likely that tactile contact with conspecifics presents a strong proximate cue to join bivouacs. Returning caterpillars encountering groups of bivouacked conspecifics often stopped searching and joined the group even if the bivouac was not the same one these caterpillars occupied previously, though we observed restlessness in some bivouacked larvae, which eventually moved on and joined other bivouacs. Accordingly, bivouac sites or locations were often reused in our study, but the individuals making up the groups assembling at those bivouac sites changed to some degree each day. Our observations suggest, then, that *A. armida*'s use of trail pheromone in their daily descent from the canopy is not highly precise, a condition that may arise from the rough texture of the bark substrate of hosts like *G. ulmifolia*. The combined effect of trail pheromone and tree shape makes relocation of conspecifics likely, however. It should be pointed out that the relatively small size of the groups observed in our study is not unusual: field observations of large intact colonies showed that small "satellite" subgroups of larvae regularly form separately from the main colony. We could not mark and track individuals in these colonies due to the size of the tree they occupied, but it is likely that the makeup of the satellite subgroups similarly changed over time judging from observed changes in group size and location.

Beyond the shift to nocturnal foraging, *A. armida*'s temporal shift in foraging behavior is of further interest in that the larvae feed solitarily at night. In early instars the caterpillars are aggregated at all times. Late-instar bivouacked larvae mobilize and ascend to the canopy at roughly the same time and clearly follow chemical trails as they do so. The near simultaneity of mobilization and use of chemical trail markers might suggest that the group remains more or less together in the canopy, but we found no evidence of this. After ascending to a certain point, many larvae appeared to go their own way, and pre-dawn position checks of larvae in one of our study groups showed only solitary feeding. This, too, is likely a stochastic dynamic, and as large colonies move to the canopy to feed it is probable that loose groupings occur, but over the course of feeding through the night the larvae increasingly spread out. *A. armida* is convergent with Australian *Perga* sawflies in this general foraging pattern. *Perga* spp. (Pergidae) rest in diurnal aggregations on the branches or trunk of their *Eucalyptus* host trees but forage solitarily at night (Evans 1934, Carne 1962). Unlike *A. armida*, *Perga* larvae are thought to relocate resting groups with acoustic cues generated by tapping the substrate with their sclerotized anal plate. It remains to be determined if other

TABLE 3. Reuse of diurnal bivouac sites on *Guazuma ulmifolia* by *Arsenura armida* caterpillars on 7 consecutive days of observation.

	Bivouac site								
Day	A	B	C	D	E	F	G	H	I
1	•	•	•	•	•	n/a	n/a	n/a	n/a
2	–	–	•	•	•	•	n/a	n/a	n/a
3	–	•	–	•	•	–	•	n/a	n/a
4	–	•	–	•	–	–	•	n/a	n/a
5	–	•	–	•	•	–	–	•	n/a
6	–	•	–	*	–	–	–	–	•
7	–	•	–	–	*	•	–	–	•

• = site occupied by ≥2 larvae.
* = site occupied by singleton.
– = site not occupied.
n/a = site not yet established.

Neotropical Lepidoptera that rest in aggregations diurnally and forage nocturnally (for example, the saturniid *Dirphia avia* (Cramer) or the papilionid *Papilio anchisiades* Esper) remain cohesive in the canopy at night or forage solitarily.

Why does *A. armida* change foraging strategy so dramatically in the 4th instar? Caterpillar foraging strategy—encompassing among other things food plant specificity, shelter building, sociality, feeding position and periodicity—is shaped by the joint effects of phylogenetic history, larval nutritional ecology, size or apparency, and defensive ecology (see reviews in Stamp & Casey 1993). Lepidopteran larvae may be expected to experience a shifting milieu of selective pressures associated with these factors as they age, particularly when growing significantly in size and biomass, and hence apparency. Accordingly, some species shift defensive strategy over time, and such shifts may be manifested in both coloration and/or behavior (Booth 1990, Montllor & Bernays 1993). For example, larvae of many swallowtails (*Papilio* and *Pterourus* spp.) are described as cryptic mimics of bird-droppings in early instars and switch to aposematism or aggressive mimicry in later instars, a coloration change that is not accompanied by a change in foraging behavior, while species like *Uresiphita reversalis* (Guenee) (Pyralidae) and *Chlosyne lacinia* (Geyer) (Nymphalidae) experience changes in foraging behavior as well as coloration over time (Stamp 1977, Bernays & Montllor 1989). Similarly, Cornell et al. (1987, 1988) found that caterpillars of the buckmoth *Hemileuca lucina* Henry Edwards, another social saturniid, exhibit behavioral changes that appear to be driven by predation: buckmoth caterpillars become less aggregative with age as they shift from predominantly defensive to escape behaviors, apparently in response to changes in predator milieu (biting predators vs. parasitoids).

Predation and/or parasitism have presumably played a role in the striking ontogenetic coloration and behavioral changes of *A. armida* caterpillars. This species is avoided by most caterpillar-hunting visual predators in the ACG dry forest, including birds and monkeys, and one of us observed that late instar larvae are lethally toxic to trogon (*Trogon elegans* Gould) nestlings when swallowed (DHJ unpublished obs.). Moreover, *A. armida* is attacked by few parasitoids. In several years of mass rearing at the ACG, by far the most abundant parasitoids are the tachinid *Winthemia subpicea* and, less commonly, the ichneumonid *Barylypa broweri* (Heinrich) (see Janzen & Hallwachs 2003 for parasitoid rearing data). The tachinid is known to hunt diurnally, and the ichneumonid is also likely to be diurnal. Elucidating the present or historical selective pressures favoring *A. armida*'s foraging strategy is contingent on correctly interpreting elements of that strategy. Is, for example, this species hiding, displaying or both when resting in large aggregations on the host trunk?

While not cryptic per se, late instars are not as brilliantly aposematic as they are in early instars (green-yellow soma ringed with black; see Janzen & Hallwachs 2003 for pictures of early instar larvae). Older caterpillars are duskier than early instars, but the intersegmental membrane is colored, giving the appearance of a dark body with narrow orange-yellow rings. In addition, late instars have a chestnut-brown head, a soma covered with fine short setae, and (until the ultimate instar) black tentacle-like protuberances on the dorsum of the thoracic segments. Given their coloration, toxicity, and grouping behavior, it seems most reasonable to conclude that late instar *A. armida* are making a group display rather than hiding (see Vulinec 1990 and Bowers 1993 for discussions of aposematic signaling strategies). This suite of traits may have different effects for different classes of predators, however. Current or past visual predators of *A. armida* may learn to avoid groups of larvae sporting colored rings, and such predators would be lacking at night when the larvae are active. Coloration is probably less important for diurnal parasitoids than other aspects of grouping. Parasitoids might be better rebuffed by caterpillars in aggregations, and even if parasitoids are unaffected by coordinated group defense (which has not been observed in *A. armida*) or larval toxicity, the caterpillars might benefit from reduced per capita parasitism rates through group dilution effects (Hamilton 1971).

It may be impossible to establish whether extant or past predators and parasitoids have selected for the foraging strategy displayed by *A. armida*. In the contemporary ecological context these caterpillars are avoided by vertebrate predators and are attacked by two diurnal parasitoids, at least in the Area de Conservación Guanacaste. One approach to test current defensive benefits of grouping would be to manipulate groups to document survivorship and parasitism rates as a function of group size. In another type of manipulation, larvae in groups of varying size could be confined to branches with a barrier that prevents them from moving to aggregation sites on the trunk. Increased rates of mortality in such groups relative to control groups moving ad libitum would suggest predation pressures currently in existence might help maintain the diurnal trunk-aggregation strategy.

It may also be informative to take a phylogenetic view. The genus *Arsenura* includes about 23 species, and *A. armida* is the only member of the genus with social larvae for all or nearly all larval instars. Some, like the Brazilian species *A. orbignyana* (Guérin-Méneville), remain gregarious in early instars and disperse afterwards (Furtado 2001a), while most others are solitary in all instars. Solitariness is almost certainly an ancestral behavioral trait in the genus judging by its widespread occurrence in other Arsenurinae, including *Titaea*, *Loxolomia*, *Coniopteryx*, and *Caio* (Wolfe & Pescador 1994, Wolfe & Bénéluz 1997, Furtado 1998, 1999, 2001b). Costa et al. (2003) speculated that the pheromone-based trail following behavior demonstrated for *A. armida* may have its origins in individual trail marking by solitary progenitors. This hypothesis also has relevance for the late-instar foraging shift reported here for *A. armida*, as at least some solitary congeners show parallel ontogenetic changes in foraging strategy. For example, *A. batesii* Druce, which is solitary in all instars, forages diurnally in the canopy in early instars, remaining on foliage, but in the penultimate instar reportedly switches to resting on the trunk by day and moving to the canopy at night. The behavioral change is accompanied by a color change from mottled brown and green to cryptic brown. If the caterpillars return to the same resting site, they may use a trail pheromone to find their way much like that described for solitary caterpillars of the charaxine butterfly *Polyura pyrrus* (Fabricius) (Tsubaki & Kitching 1986). In general this foraging switch is not uncommon in Neotropical Lepidoptera (DHJ pers. obs.), and may mean *A. armida*'s shift is an ancestral trait, albeit one that is expressed in a new, social, context.

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