Social Behavior of Larvae of the Neotropical Processionary Weevil *Phelypera distigma* (Boheman) (Coleoptera: Curculionidae: Hyperinae)

James T. Costa*, Terrence D. Fitzgerald†, Alfonso Pescador-Rubio‡, Jonathan Mays* & Daniel H. Janzen§

*Department of Biology, Western Carolina University, Cullowhee, NC;
†Department of Biological Sciences, SUNY Cortland, Cortland, NY, USA;
‡Universidad de Colima, Centro Universitario de Investigación y Desarrollo Agropecuario, Colima, Mexico; §Department of Biology, University of Pennsylvania, Philadelphia, PA, USA

Abstract

Socially gregarious behavior among free-living leaf-eating insect larvae occurs mostly among Lepidoptera, Symphyta, and a few Chyrsomelidae (Coleoptera). However, the Neotropical hyperine curculionid *Phelypera distigma* has also evolved this lifestyle, exhibiting a suite of social behaviors unique among beetles. The larvae are nomadic processionary foragers that punctuate foraging bouts with rosette-shaped resting formations (cycloalexy). Larvae also vibrate or bob their heads rapidly when moving, especially when in contact with conspecifics, and this suggests acoustic or vibrational communication. In this study we used observational and experimental approaches to investigate the basis of processionary, cycloalexic, and head-vibration behavior of this species. Larvae used both trail pheromones and thigmotactic signals to organize themselves into head-to-tail processionary columns. The trail pheromone, produced from the center of the abdomen, remains active for up to 4 h. Processions are not consistently led by particular individuals, but dynamically change over time and often temporarily break into two or more subprocessions. Subprocessions reunite through use of the trail pheromone. We found no evidence that head-bobbing generates attraction through substrate-borne or acoustic signals, but this behavior functions in direct contact to excite group activity. Time-lapse videography used to analyze cycloalexic group formation showed that larvae transition from feeding in a line along the leaf margin to cycloalexic formations on the upper leaf surface via a coordinated back-up movement that brings the posterior tip of their abdomens into contact. We identify three phases of cycloalexic formation: line-up, back-up, and an adjustment phase. Complete assembly can be achieved in as little as 5 s, but often the two phases establishing the basic rosette lasts 5–10 min, while the adjustment phase slowly

tightens the group over a period of up to an hour. Collectively these studies present the first documented case of chemical trail marking in a beetle, and provide insight into a remarkable social-behavioral repertoire convergent in key respects with the better-studied social caterpillars and sawflies.

Corresponding author: James T. Costa, Department of Biology, Western Carolina University, Cullowhee, NC 28723 USA. E-mail: costa@wcu.edu

Introduction

Larvae of several groups of leaf-eating insects – Lepidoptera, Symphyta (Hymenoptera), and Chyrsomelidae (Coleoptera) – have converged on a phytophagous lifestyle that includes group living (sociality). Sociality in these insects is thought to confer a variety of benefits, including group defense, facilitated host exploitation, and group thermoregulation (Grégoire 1988; Fitzgerald 1993; Costa & Pierce 1997). There is growing evidence that factors promoting the evolution of sociality in these groups may be more important than kinship factors in social evolution (see Costa & Fitzgerald 1996; Costa & Ross 2003). Accordingly, better documentation of the range and diversity of social forms and means of communication among group-living non-eusocial species will lead to a better understanding of social-evolutionary pathways in these groups. Here we describe the behavior of the first known social weevil larva.

Of particular interest regarding social phytophages – which are often larval societies – is how the members of colonies maintain cohesion and coordinate such activities as group defense, foraging, or nestbuilding. Mechanisms of group foraging have received the most scrutiny. In many social species contact with group members is maintained via trail pheromones, including, for example, the eastern tent caterpillar (*Malacosoma americanum*, Lasiocampidae) (Fitzgerald & Peterson 1988), the madrone caterpillar (*Eucheira socialis*, Pieridae) (Fitzgerald & Underwood 1998), the small eggar moth (*Eriogaster lanestris*, Lasiocampidae) (Ruf et al. 2001), the arsenurine caterpillar *Arsenura armida* (Saturniidae) (Costa et al. 2003), and the red-headed pine sawfly (*Neodiprion lecontei*, Diprionidae) (Costa & Louque 2001). Acoustic cues appear to be used less commonly, but are reported to occur in Australian pergid sawflies (Carne 1962), although experimental demonstration is lacking, and the European striped alder sawfly *Hemichroa crocea* (Tenthredinidae) (Hograefe 1984). Tactile cues constitute another important means of communication, often in combination with other cues. Tactile contact probably promotes grouping or foraging in many social caterpillar and sawfly species (see, for example, Costa et al. 2003; Flowers & Costa 2003), but processionary behavior is a unique form of coordinated group movement with tactile elements. Processions form when individuals maintain close front-to-rear contact as they walk in linear formations (columns). In the two processionary species thus far subject to detailed study, larvae of the Neotropical saturniid *Hylesia lineata* and the European pine processionary *Thaumetopoea pityocampa* (Notodontidae), both thigmotactic and chemical cues play a role in maintaining processions (Fitzgerald & Pescador-Rubio 2002; Fitzgerald 2003).

The great preponderance of studies of larval societies have focused on caterpillars and, to a lesser extent, sawflies; to date there has not been a detailed behavioral analysis of group living by social beetle larvae. Among the beetles, exclusively larval sociality is largely found within the Chrysomelidae (Wade & Breden 1986; Grégoire 1988; Chattopadhyay & Sukul 1994; Damman 1994; Crowe 1995). We are not aware of any example of gregariousness in beetle larvae other than that which we report here. This study focuses on the group foraging behavior of larvae of the Neotropical weevil *Phelypera distigma* (Boheman) (Cuculionidae: Hyperinae), a species likely to be unique among weevils, and perhaps beetles in general, in the breadth of its larval group behaviors, including processionary movement.

Larval *P. distigma* are nomadic foragers (sensu Fitzgerald & Peterson 1988), constructing no shelters and moving in small herds over the host tree. Larvae travel in processions when moving between feeding sites, and rest on leaves between feeding bouts in characteristic circular rosette formations. These formations are thought to be defensive in nature (the formation is termed cycloalexy by Jolivet et al. 1990). We here report the results of experimental and observational studies aimed at elucidating the basis of processionary behavior and cycloalexic group formation in *P. distigma*. We address (i) group size and movement dynamics on the host, (ii) the role of trail pheromones in processionary behavior, (iii) procession order and movement patterns, (iv) larval head-bobbing behavior, and (v) the behavioral sequence leading to cycloalexic group formation. Fitzgerald et al. (2004) present a more detailed study of the trail-marking and processionary behavior of this species.

Materials and Methods

Overview of *P. distigma* Natural History

The genus *Phelypera* belongs to the widespread weevil subfamily Hyperinae (combined with Brachycerinae by Lawrence & Newton 1995). *Phelypera* is an exclusively Neotropical genus with 14 species (Wibmer & O'Brien 1986). *Phelypera distigma* larvae feed only on the leaves of *Guazuma ulmifolia*, Sterculiaceae (Guácimo) (see records in http://janzen.sas.upenn.edu), a common secondary successional tree in lowland tropical dry forest that extends from western Mexico to Panama. It diapauses as free-living adults hiding in crevices and rolled leaves for the last 5 mo of the 6-mo rainy season and the entire 6-mo dry season. It mates with the onset of the rains in mid-May and oviposits on twigs of the host plant. The larvae feed on the young 1–3 wk old leaves and complete their development in 12–14 d. They then spin cocoons in a group on the underside of the leaf (Janzen 1979, 1983). Silk is extruded from the anal segment. The pupae complete development in less than a week; the adults emerge from the compound cocoon structure by eating the silk, and disperse over the next 2–5 d (J.T. Costa & T.D. Fitzgerald, pers. obs.) in search of hiding places. They do not visit flowers or other food sources during the next 11 mo (D.H. Janzen, pers. obs.).

Study Sites

Populations of *P. distigma* were studied in localities in Costa Rica and Mexico. The Costa Rican population was studied June 2002 at the Tropical Dry Forest Research Station, Sector Santa Rosa of the Area de Conservación Guanacaste (ACG), northwestern Costa Rica (10°84′N, 85°62′W). In July 2002 and 2003 studies were conducted at the Estación de Biologia Chamela (UNAM), Jalisco, Mexico (19°31′N, 105°03′W); some specimens were collected east of Manzanillo, Mexico, at 19°03′N, 104°12′W. Colonies were studied on *G. ulmifolia* trees in the field or transferred to fresh branch cuttings for laboratory studies; all studies were conducted under ambient conditions with larvae exhibiting normal phenology.

Group Foraging and Trail Following

Twenty-four larval groups and 25 pupal groups were selected at random and all individuals counted to obtain mean group size. Frequency of feeding and movement between feeding sites was documented for 12 undisturbed field colonies, censused hourly for a total of 20 h (two periods of 9 and 11 h of continuous monitoring over 2 d).

Groups were observed moving over bridges between exhausted and new food patches, permitting us to analyze degree of group cohesiveness as larvae colonize new feeding sites. In each of nine trials, a group of 20 sibs was set up on fresh food and permitted to feed ad libitum. When the food was exhausted, the larvae had to move over a 15 cm *Guazuma* branch bridge to new feeding site. The rate and manner of group movement was recorded.

We conducted group-choice Y-maze tests following the method of Costa & Louque (2001) to establish that a persistent trail marker is deposited as larvae move in processions, and that this trail marker permits straggling processions to relocate the main group. Twelve larvae were placed on a feeding site at the base of a Y-maze stem fashioned from slender (3–4 mm diameter) *Guazuma* twigs. When the group sought to abandon the site after depleting the food, the first six were permitted to walk up the Y-maze stem and one arm ('treatment arm' – the other arm was blocked with a cardboard barrier) while the last six were prevented from walking up the stem by moving their depleted site away a short distance. The first six larvae were collected onto new food at end of the treatment arm. The cardboard barrier was then removed from the control arm and the last six larvae were given access to the Y-maze. The arm choice of the lagging group was recorded; this was replicated 16 times using different groups of larvae and fresh Y-mazes and alternating treatment arms.

Processionary Behavior

We quantified the average velocity of larvae moving in processions on paper by setting up five processions of 4–5 larvae each on white paper. Each column was permitted to move ad libitum under ambient temperatures (30–32°C), and the position of the head of the lead larva was marked, to one side, at 1-min intervals

with a light pencil mark. We averaged the distance moved per minute to obtain average velocity.

To test if certain larvae consistently adopted or maintained leader or follower positions in processions, six larvae were given unique marks with non-toxic acrylic enamel paints (Gloss^{TM}, Plaid Enterprises, Inc., Norcross, Georgia, USA) and permitted to form a procession in a circular arena. The paints were applied only to the tips of the long setae of the abdomen, and larvae were observed before experimental use for 4 d post-marking and we saw no indication that larval survivorship and feeding were affected. The position order of each marked larva was recorded at 5-min intervals for 1 h. This was repeated for nine groups.

Processionary behavior was further explored in experiments where the leader, second in procession, or last in procession was removed and the effects on the procession observed. Although they would not be naturally experienced in the field, such manipulations help establish the relative priority of chemical and tactile cues for larvae in different positions in processions, and the degree to which larvae can act independently of the group. The behavior of individuals directly before or behind the affected individual (unaffected, stopped moving, abandoned procession) was recorded in each of 15 trials.

Cycloalexic Group Formation

Phelypera distigma larvae typically rest in distinctive rosette formation, with heads pointed outward and posterior end of the abdomen inward (Fig. 1). This resting posture, described for just a few gregarious insect groups (see Jolivet et al. 1991; Vasconcellos-Neto & Jolivet 1994), including *P. distigma* (Jolivet & Maes 1996), has been little studied in terms of the coordination of larval movements that achieve the often remarkably symmetric circular formations. To better understand how *P. distigma* larvae transition between feeding along the leaf margin to cycloalexic group formation, and vice versa, we employed video analysis of 12 laboratory groups using a wireless video camera (x10 Inc., model VR36A, x10 Wireless Technology, Inc., Kent, Washington, USA) and time-lapse video recorder (Philips Hi-Resolution S VCR, Philips Communication, Security & Imaging, Inc., Atlanta, Georgia, USA).

Acoustic or Substrate-Borne Signaling

We noted that *P. distigma* larvae often exhibit a characteristic head-bobbing behavior when moving in processions (with the exception of the leader) and when positioning themselves into or breaking out of resting groups. At these times they move their heads up and down rapidly and continuously. Fitzgerald et al. (2004) estimate, from video analysis, that larvae bobbed heads approximately five times per second. We tested the possibility that *P. distigma*'s head-bobbing generates acoustic or vibrational signals that attract other larvae, as has been suggested (though not tested) for processionary pergid sawflies (see Evans 1934; Carne 1962).
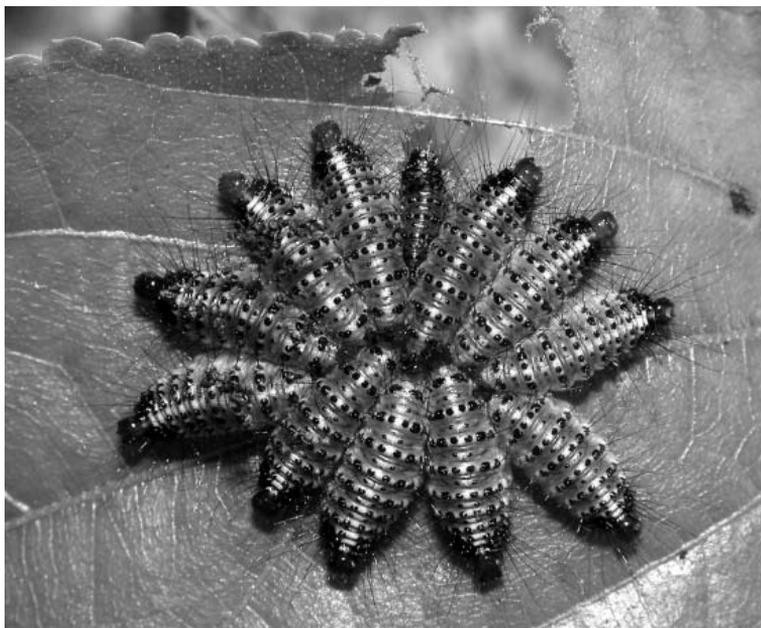
Fig. 1: Group of *Phelypera distigma* larvae resting in characteristic rosette or cycloalexic formation on the upper surface of a *Guazuma ulmifolia* leaf

In our test, a fresh *G. ulmifolia* twig 7.5 cm long was divided into two zones: (i) a 'stridulation' zone 2.5 cm in length, and (ii) a 'test zone' 5 cm in length, separated by a paper screen closely situated to but not touching the twig (to eliminate visual cues). The test zone was enclosed on the opposite end by a similar screen to keep larvae from wandering off the apparatus. Eight late instar *P. distigma* larvae were placed in the stridulation arena and prodded with a fine brush to stimulate movement and head-bobbing behavior. A single mid-instar test larva was then placed in the center of the test arena. After 3 min the position of the test larva was recorded: twig half in the direction of the stridulating group vs. the opposite half away from group. This was repeated for 15 trials.

Results and Discussion

Group Foraging and Trail Following

In our Costa Rica study population, *P. distigma* groups averaged 13.25 ± 2.14 individuals (N = 24 groups; values throughout are reported as $\bar{x} \pm SE$). Each group is apparently made up of sibs, unless there has been group merging. Pupal groups declined to an average of 7.72 ± 1.25 individuals (N = 25 groups), which may be due to mortality, a decline in group cohesiveness, and/or stochastic fragmentation by the terminal instar. Some group fragmentation in late instars may stem from fewer large intact leaves as larvae grow, making it harder

for large groups to rest and feed in a cohesive mass. However, our observations suggest that group splitting is uncommon, and smaller average group size in late instars is probably due to mortality.

Although subsets of larvae in a group often leave depleted sites in advance of their group-mates, the group that follows rarely fail to join their group-mates. The 12 groups we tracked in the field changed feeding sites a total of 26 times over the 20-h observation period. Only one time was there a coalescence and fragmentation event in this time interval despite relocating at distances up to a meter. After exhausting a feeding site larvae move en masse to new site that is usually adjacent, but apparently acceptable leaves are often passed over for somewhat more distant leaves. The mean distance between feeding sites in the field was 39.9 ± 6.4 cm measured petiole-to-petiole from exhausted to new leaves.

Our observations of group movement in the laboratory were consistent with the foraging dynamic observed in the field. These studies showed that groups may initially fragment as subgroups of larvae move to new feeding sites, but lagging groups eventually catch up. In observations of movement rates of nine groups of 20 larvae moving over a 15-cm bridge, the group never moved as a single long procession. Two or more subprocessions was the norm, and as a result the first 10 larvae (the first half of the group) had arrived at the new feeding site in an average of 8.4 ± 1.8 min from the time the bridge was first contacted, but the last of the larvae (the remaining half of the group) had not arrived until 38.9 ± 6.3 min after first contact.

The eventual cohesion of colonies despite separation suggests the use of trail-based chemical communication, and group-choice Y-maze experiments confirmed this to be the case. In 16 Y-maze trials, 14 test groups selected the treatment arm traversed by a small column of larvae, one selected the control arm, and one group was scored as a split choice, indicating a strong preference for substrate previously contacted by conspecifics (χ^2 test, p = 0.0008) (Table 1). Silk is not produced by larvae as they move in processions, and thus plays no role in this trail-following response. Fitzgerald et al. (2004) show that trails are not long-lived. Trail age and relative strength experiments showed that trails remained active after 0.5 h but lost activity by 4 h. In the group Y-maze experiment reported in this paper treatment arms proved attractive about 1 h post-contact with a small larval procession, indicating activity lasts at least this long. In terms of relative strength of trails marked (or at least traversed) by different numbers of larvae, larvae have a strong preference for trails left by 10 vs. one conspecific, but trails left by 10 vs. five conspecifics were chosen with equal frequency (Fitzgerald et al. 2004). This suggests there may be a threshold level of trail marking above which larvae do not continue to mark, or, if marking is passive, above which larvae do not differentiate.

Processionary Behavior

We measured a total of 18 processionary tracks for the five study groups (Table 2), yielding an average procession velocity of 4.5 ± 0.73 cm/min.

Table 1: Group Y-maze arm choice. Test processions of larvae were scored as selecting the treatment arm previously contacted by a procession of conspecifics (T), the blank control arm (C), or as a split choice (S) with some larvae selecting the treatment arm and some the control arm. Test groups were permitted to move ad libitum over the maze, resulting in a time lag between contact with the first procession and contact with the test procession

Trial	Arm choice[a]	Time lag (min) between marking and test groups
1	T	22
2	T	53
3	T	47
4	T	57
5	T	3
6	C[b]	20
7	S[c]	9
8	T	15
9	T	22
10	T	24
11	T	1
12	T	8
13	T	11
14	T	6
15	T	14
16	T	2

[a]$\chi^2 = 11.27$; p = 0.0008.
[b]A single larva breached the barrier to the control arm approx. 10 min prior to the movement of the entire test group; this larva apparently influenced the subsequent arm choice.
[c]Split choice occurred as a result of exploration of a portion of the control arm by some test larvae; this is dropped from chi-square for lack of clear arm choice.

Individual *P. distigma* larvae in processions exhibit no consistent leader/follower behavior, and procession order dynamically changes over time. We found an average of 4.2 ± 0.24 different larvae occupied the leader position during the 1-h observation period, with an average of 5.8 ± 0.47 lead changes (Fig. 2). The precise cause of lead changes is not clear. In some cases the leader halted for unknown reasons and larvae in the rear seemed to push ahead until one of them broke out of the linear formation and took the lead.

Experiments in which larvae in various positions in processions were removed helped clarify the relative roles of chemical and tactile stimulation in processions. We found that removal of the leader has little effect on processions; the second larva in line assumes leader position and processions keep moving. Significantly, the second larva often advanced a few millimeters to the approximate midpoint position of the leader before it was removed. At this point some of the larvae (nine of 15 trials) briefly stopped and swept their head back and forth perpendicular to the direction of movement, suggesting they lost a chemical cue at that point; this is consistent with a midabdominal secretion site

Table 2: Average velocity (cm/min) of five processions of *Phelypera distigma* larvae recorded in the laboratory on clean white paper substrate

| Group | Distance covered (cm) in 1-min intervals | | | | | Average |
	1	2	3	4	5	
1	4.0	3.5	4.3	–	–	3.93
2	7.6	7.3	–	–	–	7.45
3	2.9	4.0	4.0	3.6	3.0	3.74
4	5.0	4.1	3.6	3.0	–	3.93
5	4.9	4.7	2.5	2.4	–	3.63

Mean velocity $\pm$ SE = 4.54 $\pm$ 0.73.
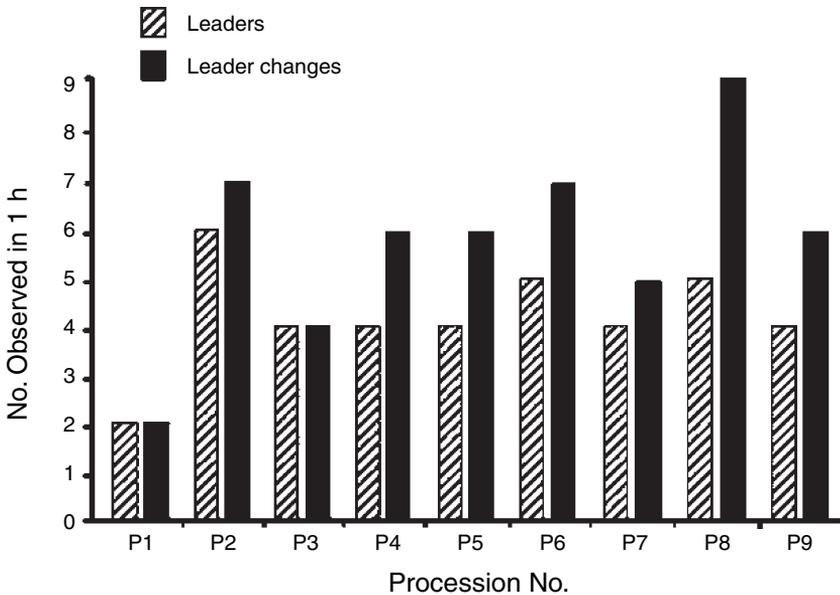
Fig. 2: Number of individual procession leaders (hatched bars) and leader changes (solid bars) for nine processions consisting of six uniquely marked *Phelypera distigma* larvae, each observed in a circular arena for 1 h. Procession leaders change frequently, which indicates that processions are not consistently led by particular individuals

for the trail pheromone of *P. distigma*, as reported by Fitzgerald et al. (2004). Despite this hesitation, the time taken by second larvae in line to reach the position of the leader (one body length) was no different on average whether the leader was removed or undisturbed, although the variance in time was doubled in leader-removed treatments (13.33 $\pm$ 1.51 s leader removed, 13.25 $\pm$ 0.72 s leader intact). The increased variance in time with removal of the leader is attributable to loss of stimuli and, perhaps, disturbance.

Removal of the second larva in a procession leads to the immediate halt of the leader ahead, but not of those in the procession behind. The leader stopped and remained motionless in all of 15 trials where the second larva was removed, and only moved again when the next larva in the procession caught up to and touched it in 14 of 15 trials. In no case did the removal of the last larva in a procession result in the halting of the procession.

These results suggest that processioning larval *P. distigma* largely rely on tactile and, to a lesser extent, chemical cues, to maintain the structure of a procession. It appears that as long as contact is maintained forward or rear the larvae will continue to press forward in processionary formation. Removal of any larva except the second in line permits all remaining larvae to maintain contact with conspecifics anteriorly and/or posteriorly. Accordingly, they continue to procession, albeit in subprocessions in cases where a centrally situated larva is removed. Removal of the second larva, on the other hand, leaves the leader without any stimulus from the rear or front, hence its abrupt halt, while the third in line still has contact to its posterior and so is stimulated to keep moving. The chemical trail marker may facilitate this process: the path for the new leader is not virgin terrain, but marked a short distance.

Acoustic or Substrate-Borne Signaling

The results of our stridulation arena test suggest there is no acoustic or substrate-borne attractive signal generated by *P. distigma*'s rapid head-bobbing behavior. Six larvae selected zone a, five selected zone b, and four were in the center of the test arena ($\chi^2 = 0.091$, p = 0.763). This striking behavior is likely to play a communicative role, but probably at very close range or in direct contact where it functions to excite group members to activity (see Fitzgerald et al. 2004).

Cycloalexic Group Formation

The highly distinctive circular rosette formations of *P. distigma*, which occur at nearly every resting period, may represent a defensive display. Although cycloalexy is described from a few groups besides *P. distigma*, including pergid sawflies and chrysomelid beetles (Weinstein 1989; Vasconcellos-Neto & Jolivet 1994), and certain species of hemileucine Saturniidae (D. H. Janzen, pers. obs.), the behavioral basis of rosette formation has not been reported. Video analysis of our study of *P. distigma* groups revealed that larvae achieve cycloalexic groups although a behavioral sequence that includes three phases we will refer to as (i) line-up, (ii) back-up, and (iii) adjustment. Figure 3 illustrates the positioning process for two representative groups videotaped in the laboratory, both of which moved into rosette formations in < 10 min.

Cycloalexic group formation is nearly always preceded by the side-by-side positioning of most or all of the larvae in a group. This 'line-up' phase occurs whether the resting group forms immediately following a feeding bout or procession. Some of the larvae then back up, backing along side others in their
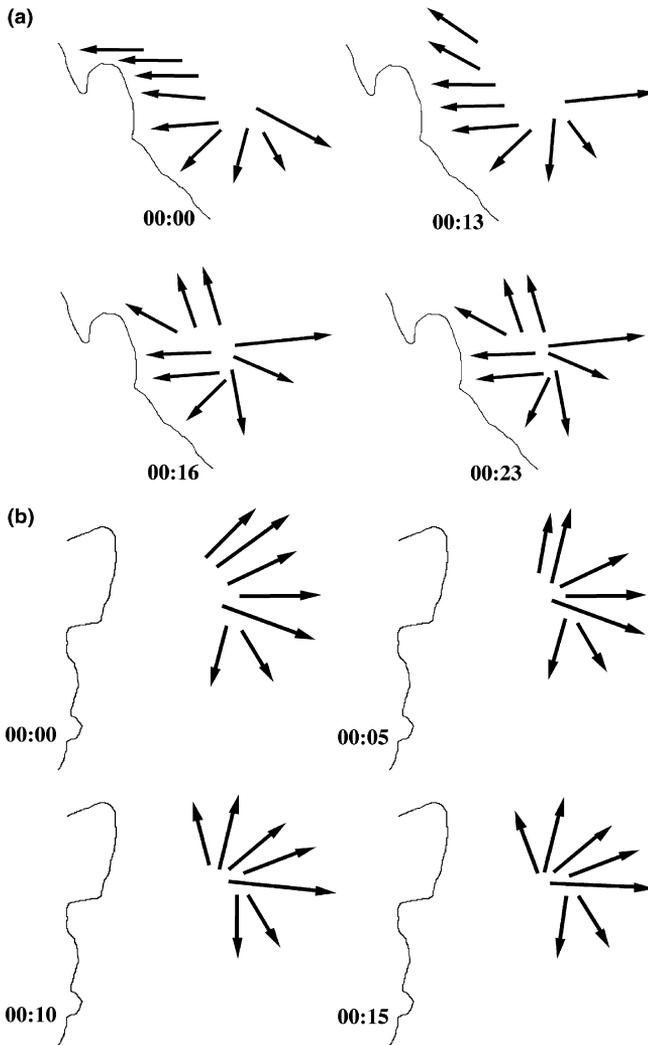
Fig. 3: Schematic diagrams for two representative *Phelypera distigma* groups transitioning to cycloalexic (rosette) resting formations. Arrows denote individual larvae with arrowheads indicating the heads; for scale, the longest arrows in the diagram correspond to larvae approximately 1 cm in length. The continuous line to the left of each group represents the margin of a *Guazuma ulmifolia* leaf where larvae had been feeding. Diagrams are based on still-frame tracings of time-lapse video footage, taped at 0048 h speed. The times given in the figure are real-time minutes converted from the video. Note that larvae are initially arrayed more or less in a row (phase 1, see text), after which individuals back up alongside each other until contacting others with the posterior tip of the abdomen (phase 2). The initial rosette (through phase 2) was formed within 10 min for these groups, during which some larvae moved more than did others. One or more larvae in a group may continue to refine their position for as much as an hour (phase 3)

group until their posterior ends contact. Some larvae often back greater distances than others, and halt once making posterior contact. Larvae often maintain lateral contact through this process as well, but lateral contact is variable and perhaps of secondary importance, while there is always posterior contact when they come to rest. This is clear in cycloalexic formation of groups as small as 3–5 individuals. Larvae in such groups also stop positioning themselves once the posterior tip of their abdomen is in contact with the rear of a conspecific, but there are too few larvae to contact neighbors laterally as well, giving the whole a radiating wheel-spoke appearance with a large space between the larvae. It should be noted, however, that we have on occasion observed field colonies resting in a ring formation, with larvae in close lateral but not exclusively posterior contact. The third phase consists of an adjustment period, as some larvae jostle and reposition, presumably to better fit into the rosette formation. Although the adjustment period can be lengthy, the behavioral sequence of phases 1 and 2 can be completed in a few minutes and in an orderly manner. Video analysis of individual larval positions in linear-to-rosette transitions shows how feeding or resting aggregations can rapidly collapse into cycloalexic formations (Fig. 4).

The results of this study and that of Fitzgerald et al. (2004) show that processionary behavior in *P. distigma* consists of both thigmotactic and chemotactic components, much like the processionary lepidopterans *Hylesia lineata* and *Thaumetopoea pityocampa* (Fitzgerald & Pescador-Rubio 2002; Fitzgerald 2003). This dual communication mode differs from the tandem running behavior found in many termite and ant genera. Ants that employ tandem running in recruitment or colony relocation move in leader-follower pairs, the follower maintaining direct antennal contact with the leader. A calling pheromone may help initiate tandem running or reunite separated pairs, but the tactile link is paramount (Hölldobler & Wilson 1990). Unlike tandem running ants, *P. distigma* processions are maintained by thigmotaxis (even dead models can elicit following; see Fitzgerald et al. 2004) and chemical trails. The trail pheromone is also likely used to enable isolated individuals or small groups to relocate the main colony as the group moves among feeding sites on the host tree. The staggered manner in which groups moved between feeding sites in our study suggests that brief periods of separation of subgroups are likely to arise frequently, and trail marking aids in reunion of separated groups. The characteristic head-bobbing motion made by larvae (excepting the leader) while in processions likely functions to indicate mutual presence and stimulate group activity; in processions, this stimulation may induce individuals to keep moving.

Phelypera distigma's social behavior repertoire is not known for other weevils or beetles. Indeed, there is only one reported case of trail-marking behavior in a larval beetle, namely the chrysomelid willow leaf beetle *Plagiodera versicolora* (Laicharting) (M. Wade, pers. com.). As larval group living is common among chrysomelids, however, it is likely that other species employ chemical and/or tactile communication in group foraging. In their review of cycloalexy in
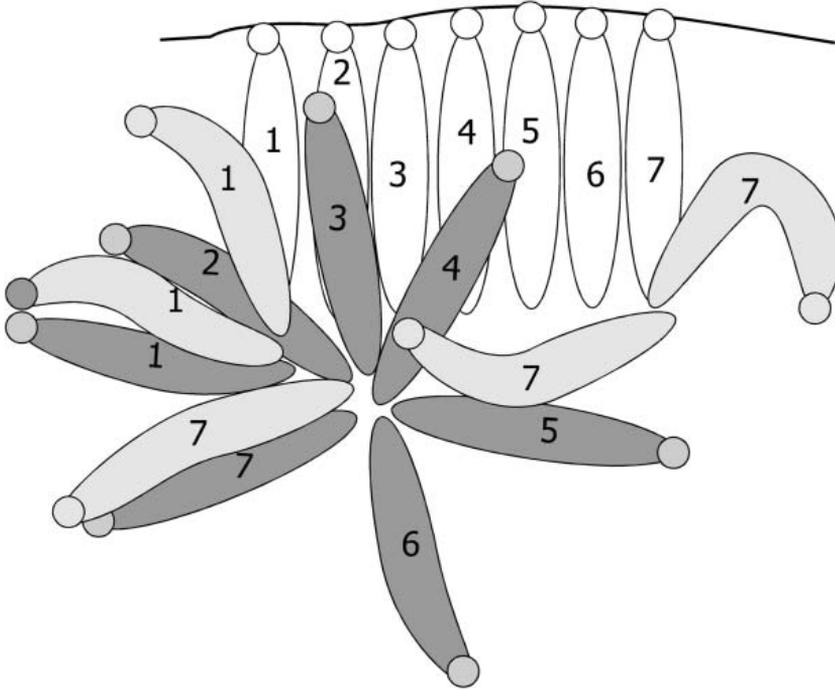
Fig. 4: Schematic diagram illustrating in greater detail the orderly transition (light shading) between a leaf-edge feeding aggregation (unshaded) of *Phelypera distigma* and a cycloalexic formation (dark shading). Note that both the feeding and resting groups are orderly larval arrangements. The first larva to move back from the feeding formation was larva 7 which followed the pathway depicted in the illustration. Larva 1 rotated into position next using the depicted movement pattern. Larva 2 moved in near unison with larva 1, and used the same pattern of movement. Larvae 3–6 continued to feed briefly then 3 and 4 backed up slightly to their positions in the rosette and 6 and 5, using the movement pattern depicted for larva 7, moved into the rosette formation. The total time lapsed between the initial movement of larva 7 from the feeding aggregation until the last larva was positioned in the rosette was 5 s

chrysomelids, Vasconcellos-Neto & Jolivet (1994) suggest that cycloalexy is often linked to parental care. This is not the case with *P. distigma*, adults of which do not co-occur with the larvae (Janzen 1979). The group most closely convergent with *P. distigma* appear to be the pergid sawflies of Australia, which exhibit both processionary behavior and cycloalexy. Maternal defense of pergid larvae, first reported in the early nineteenth century by Lewis (1836), also occurs in this group. It is unclear if pergids also employ chemical trail markers in their processions.

Cycloalexy is thought to play a role in larval defense. It may be an aposematic display aimed at vertebrate predators in that the larvae are conspicuously marked in black and light beige/gray, and the groups are ostentatiously positioned on the upper as well as lower surfaces of the leaves. The larvae (and their cocoons) are ignored by the large numbers of foliage-gleaning birds in their habitat. With respect to invertebrate predators, we can only

observe that *P. distigma* larvae are not harvested by polistine wasps, ants, spiders and other generalist predators that readily harvest caterpillars in dry forest habitats (D. H. Janzen, pers. obs.). However, there is one species of pentatomid bug that is not deterred by intrinsic or behavioral traits of the weevil larvae. In field and laboratory observations in Costa Rica we frequently (>20 occasions) observed juveniles of an unidentified asopine pentatomid successfully attack *P. distigma* larvae in cycloalexic groups. In a common attack sequence, the hemipteran slowly approaches and sometimes circles the weevil group, then advances with beak extended. A larva is typically stabbed just behind the head and dragged from the group a short distance on the same leaf and consumed. These attacks were observed to provoke group pulsations and/or head-bobbing, but all bugs we observed were successful in preying on a weevil larva. The distinctive head-outward formation may not in itself be functional in reducing predation, but the larvae may enjoy a per capita reduction in predation probability simply by grouping (Hamilton 1971). *Phelypera distigma* larvae suffer conspicuously trivial frequencies of parasitoids, with far $<1\%$ being attacked by tachinid flies and there being no hymenopterous parasitoids (http://janzen.sas.upenn.edu).

Much remains to be learned of *P. distigma*'s social behavior, particularly the precise function of the pulsation and head-bobbing behaviors, the defensive efficacy of cycloalexic group formation against predators, group pupation behavior, and the chemical nature and secretory site of its trail pheromone. This remarkable weevil surely ranks as one of the behaviorally oddest beetles yet studied, with its processionary foraging, circle-the-wagons defensive formations, and group pupal masses spun of silk exuded from distinctive anal glands. Better understanding the convergent and unique aspects of *P. distigma*'s social repertoire will aid our understanding of larval social evolution in general, as studies of the mechanisms, costs and benefits of group living in beetles such as this are considered along with the more plentiful studies of their distant relatives in other orders.

Literature Cited

Carne, P. B. 1962: The characteristics and behaviour of the saw-fly *Perga affinis affinis* (Hymenoptera). Aust. J. Zool. **10**, 1—38.

Chattopadhyay, A. K. & Sukul, N. C. 1994: Anti-predator strategy of larval aggregation pattern in *Aspidomorpha miliaris* (Chrysomelidae: Coleoptera). Entomon **19**, 125—130.

Costa, J. T. & Fitzgerald, T. D. 1996: Developments in social terminology: semantic battles in a conceptual war. Trends Ecol. Evol. **11**, 285—289.

Costa, J. T. & Pierce, N. E. 1997: Social evolution in the Lepidoptera: ecological content and communication in larval societies. In: The Evolution of Social Behaviour in Insects and Arachnids (Choe, J. C. & Crespi, B. J. eds). Cambridge University Press, Cambridge, UK, pp. 407—442.

Costa, J. T. & Louque, R. W. 2001: Group foraging and trail following behavior of the red-headed pine sawfly *Neodiprion lecontei* (Fitch) (Hymenoptera: Symphyta: Diprionidae). Ann. Entomol. Soc. Am. **94,** 480—489.

Costa, J. T. & Ross, K. G. 2003: Fitness effects of group merging in a social insect. Proc. R. Soc. Lond. B **270,** 1697—1702.

Costa, J. T., Gotzek, D. A. & Janzen, D. H. 2003: Late instar shift in foraging strategy and trail pheromone use by caterpillars of the Neotrophical moth *Arsenura armida* (Cramer) (Saturniidae: Arsenurinae). J. Lep. Soc. **57,** 220—229.

Crowe, M. L. 1995: Daytime mechanisms of reaggregation in imported willow leaf beetle, *Plagiodera versicolora*, larvae (Coleoptera: Chrysomelidae). Anim. Behav. **50,** 259—266.

Damman, H. 1994: Defence and development in a gregarious leaf-mining beetle. Ecol. Entomol. **19,** 335—343.

Evans, J. W. 1934: Notes on the behavior of the larval communities of *Perga dorsalis* Leach (Hymenoptera, Tenthredinidae). Trans. R. Entomol. Soc. **82,** 455—460.

Fitzgerald, T. D. 1993: Sociality in caterpillars. In: Caterpillars: Ecological and Evolutionary Constraints on Foraging (Stamp, N. E. & Casey, T. M., eds). Chapman and Hall, New York, pp. 372—403.

Fitzgerald, T. D. 2003: Role of trail pheromone in foraging and processionary behavior of pine processionary caterpillars *Thaumetopoea pityocampa*. J. Chem. Ecol. **29,** 513—532.

Fitzgerald, T. D. & Pescador-Rubio, A. 2002: The role of tactile and chemical stimuli in the formation and maintenance of the processions of the social caterpillar *Hylesia lineata* (Lepidoptera: Saturniidae). J. Ins. Behav. **15,** 659—674.

Fitzgerald, T. D. & Peterson, S. C. 1988: Cooperative foraging and communication in caterpillars. BioScience **38,** 20—25.

Fitzgerald, T. D. & Underwood, D. L. A. 1998: Trail marking by the larva of the Madrone butterfly *Eucheria socialis* and the role of the trail pheromone in communal foraging behaviour. J. Ins. Behav. **11,** 247—263.

Fitzgerald, T. D., Pescador-Rubio, A. & Costa, J. T. 2004. Trail marking and processionary behavior of the larvae of the weevil *Phelypera distigma* (Coleoptera: Curculionidae) (in press).

Flowers, R. W. & Costa, J. T. 2003: Larval communication and group foraging dynamics in the red-headed pine sawfly, *Neodiprion lecontei* (Fitch) (Hymenoptera: Symphyta: Diprionidae). Ann. Entomol. Soc. Am. **96,** 336—343.

Grégoire, J.-C. 1988: Larval gregariousness in the Chrysomelidae. In: Biology of the Chrysomelidae (Jolivet, P., Petitpierre, E. & Hsio, T. H., eds). Kluwer Academic Publishers, Boston, MA, pp. 253—260.

Hamilton, W. D. 1971: Geometry for the selfish herd. J. Theor. Biol. **31,** 295—311.

Hograefe, T. 1984: Subtrat-Stridulation bei den koloniebildended Blattwespenlarven von *Hemichroa crocea* (Geoff.) (Hymenoptera: Tenthredinidae). Zool. Anz. **213,** 234—241.

Hölldobler, B. & Wilson, E. O. 1990: The Ants. Harvard University Press, Cambridge, MA.

Janzen, D. J. 1979: Natural history of *Phelypera distigma* (Boheman), Curculionidae, a Costa Rican defoliator of *Guazuma ulmifolia* Lam. (Sterculiaceae). Brenesia **16,** 213—219.

Janzen, D. H. ed 1983: Costa Rican Natural History. Univ. Chicago Press, Chicago, IL.

Jolivet, P. & Maes, J.-M. 1996: Un cas de cycloalexie chez un Curculionde: *Phelypera distigma* (Boheman) (Hyperinae) au Nicaragua. L'Entomologiste **52,** 97—100.

Jolivet, P., Vasconcellos-Neto, J. & Weinstein, P. 1990: Cycloalexy: a new concept in the larval defence of insects. Insecta Mundi **4,** 133—142.

Lawrence, J. F. & Newton, A. F., Jr 1995: Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson (Pakaluk, J. & Slipinski, S. A., eds). Muzeum i Intytut Zoologii PAN, Warszawa, pp. 779—1006.

Lewis, R. H. 1836: Case of maternal attendance on the larva by an insect of the tribe of Terebrantia, belonging to the genus *Perga*, observed at Hobarton, Tasmania. Trans. R. Entomol. Soc. Lond. **1,** 232—234.

Ruf, C., Costa, J. T. & Fiedler, K. 2001: Trail-based communication in social caterpillars of *Eriogaster lanestris* (Lepidoptera: Lasiocampidae). J. Ins. Behav. **14,** 231—245.

Vasconcellos-Neto, J. & Jolivet, P. 1994: Cycloalexy among chrysomelid larvae. In: Novel Aspects of the Biology of Chrysomelidae (Jolivet, P., Cox, M. L. & Petitpierre, E., eds). Kluwer Academic Publishers, Boston, MA, pp. 303—309.

Wade, M. J. & Breden, F. 1986: Life history of natural populations of the imported willow leaf beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae). Ann. Entomol. Soc. Am. **79,** 73—79.

Weinstein, P. 1989: Cycloalexy in an Australian pergid sawfly (Hym., Pergidae). Bull. Ann. Soc. R. Belge Entomol. **125,** 53—60.

Wibmer, G. J. & O'Brien, C. W. 1986: Annotated Checklist of the Weevils (Curculionidae *sensu lato*) of South America, Vol. 39. American Entomological Institute, Gainesville, FL.