Journal of Insect Behavior, Vol. 19, No. 1, January 2006 (© 2006)
DOI: 10.1007/s10905-005-9007-y

Vibrational Communication in the Cherry Leaf Roller Caterpillar *Caloptilia serotinella* (Gracillarioidea: Gracillariidae)

Lynn E. Fletcher,[1] Jayne E. Yack,[2,4]
Terrance D. Fitzgerald,[3] and Ron R. Hoy[1]

Revised June 10, 2005; accepted August 10, 2005

---

*The cherry leaf roller (*Caloptilia serotinella*) produces three distinct types of substrate-borne signals—scraping, plucking, and vibrating—during interactions between conspecifics. Signals were recorded using a piezoelectric sensor, and behavioral experiments tested the hypothesis that signaling functions in territorial disputes over costly leaf shelters. Trials involving the introduction of a conspecific to a resident's leaf shelter demonstrated a significant increase in the amount of scraping by the resident; there was no significant difference in plucking or vibrating. In control trials, general mechanical disturbances such as opening and probing the shelter typically did not elicit signaling. Although both residents and intruders were observed to produce all three signal types, residents most often initiated signaling, and scraped significantly more than intruders. Implications for understanding the diversity of vibrational communication in larval Lepidoptera, particularly shelter-building species, are discussed.*

KEY WORDS: Competition; leaf shelter; caterpillar; acoustic; vibration; communication.

[1] Department of Neurobiology and Behavior, Cornell University, Ithaca, New York.
[2] Department of Biology, College of Natural Sciences, Carleton University, Ottawa, Ontario.
[3] Department of Biological Sciences, State University of New York, Cortland, New York.
[4] To whom correspondence should be addressed at Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada, K1S 5B6; e-mail: jyack@ccs.carleton.ca.

INTRODUCTION

Conspecific communication in moths and butterflies has long been the focus of scientific investigation. Species vary in the sensory modalities employed for communication, and the use of chemical, acoustic, and visual cues has been widely documented (reviewed in Hallberg and Poppy, 2003; Minet and Surlykke, 2003; Warrant *et al.*, 2003, respectively). Larval Lepidoptera also engage in conspecific interactions for purposes of group defense, foraging, and competition for resources (Costa and Pierce, 1997; Fitzgerald and Costa, 1999). However, few studies have examined these behaviors, or the underlying sensory mechanisms involved. Pheromones, particularly those associated with trail-following behaviors in processionary species, are the best documented signals for conspecific communication (e.g. Ruf *et al.*, 2001; Fitzgerald, 2003), but little is known about the roles of visual, tactile or acoustic signals in larval interactions.

The use of solid borne acoustic signals (vibrations) is thought to be widespread in many insects, including many larval forms, but the phenomenon has not been widely studied, since vibrations are generally inaudible to the human ear and difficult to detect without using specialized equipment (reviewed in Cocroft, 2001; Cocroft and Rodríguèz, 2005; Virant-Doberlet and Cokl, 2004). In one report, late instar larvae of the hook-tip moth *Drepana arcuata* (Drepanidae) were shown to use vibrational displays in defending silken leaf shelters from conspecific intruders (Yack *et al.*, 2001). In addition to several other Drepanidae species (Yack *et al.*, 2001; Yack and Hasenfuss, unpublished observations), other Lepidoptera caterpillars have been suggested to use vibrations in territorial encounters (e.g. Russ, 1969; Hunter, 1987). Territorial disputes may be widespread among caterpillars, particularly for those investing much time and energy in building and maintaining shelters or silk mats (e.g. Weyh and Maschwitz, 1982; Okuda, 1989; Berenbaum *et al.*, 1993; Poirier and Borden, 1995). For caterpillars, using acoustic displays for territorial encounters would avoid physical battles, which could result in harmful or lethal encounters when biting is involved.

The gracillid moth, *Caloptilia serotinella*, is a common leaf-roller within western New York State, feeding upon black cherry leaves, *Prunus serotina.* Late instar (third to fifth) larvae construct shelters by spinning silk and stretching it between two opposable points to curl the leaf (Fig. 1). Shelter-building activity often occurs on the outer portion of cherry branches where the leaves are younger and more malleable. The labor-intensive process of constructing a leaf shelter takes about 4–10 h to complete. Upon completion, the larva remains within the shelter, skeletonizing the leaf surface for food and eventually spinning a cocoon for pupation (Fitzgerald *et al.*,

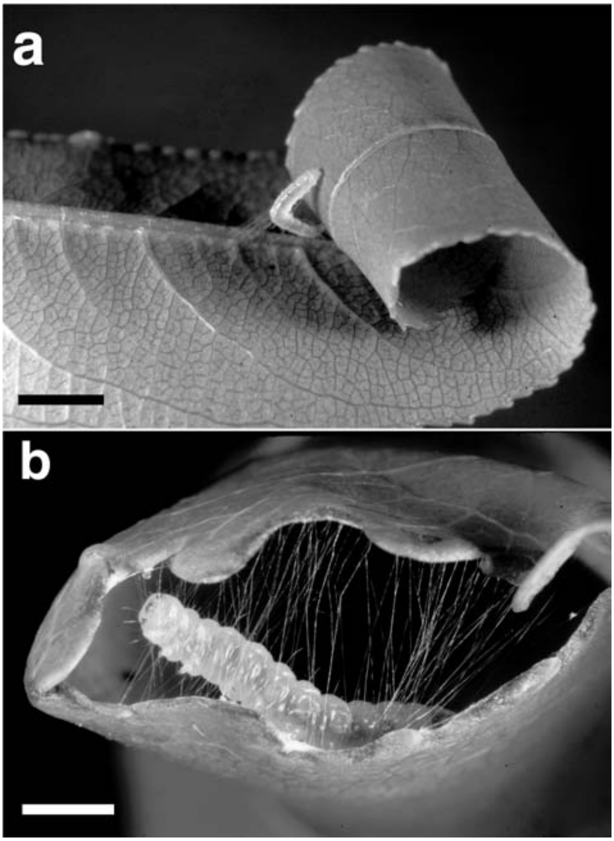

Fig. 1. A late instar *C. serotinella* constructing a leaf shelter. (a) In the early stages of shelter building, a black cherry leaf (*P. serotina*) is rolled longitudinally from its distal tip. Scale bar: 4 mm. (b) In the final stages of shelter construction, the caterpillar seals the ends of the tube with silk. Scale bar: 2 mm.

1991; Fitzgerald and Clark, 1994; Fitzgerald, 1995). While studying the leaf-shelter building behavior in this species, Fitzgerald observed what appeared to be aggressive 'tête à tête' encounters between conspecifics within leaf rolls. Although acoustic signals were not audible, it appeared that the caterpillars were signaling to one another, rather than engaging in direct physical interactions. Like *D. arcuata,* which uses acoustic signals and also invests energy in its shelter, we hypothesized that acoustic signals were being used in territorial encounters between residents and intruding conspecifics. In this paper we describe the vibrational signals, and the behavioral contexts within which they occur.

MATERIALS AND METHODS

Insects and Plants

During mid-July of 2001, the rolled leaf shelters of *C. serotinella* were collected from black cherry (*P. serotina*) trees near the college campus in Cortland, New York. Most caterpillars built leaf shelters on new leaves near the ends of branches. The cuttings were about 40 cm in length and the cut ends were placed in fresh water, where they remained turgid for 5–6 days. All behavioral trials took place on a black cherry leaf, thus providing a natural substrate for observations.

Vibration Recording and Analysis

The shelters of several caterpillars were unrolled so that their location on the leaf was visible. A ceramic phonocartridge (= piezo electric sensor) was positioned on the leaf close to the caterpillar to detect its movements and vibrations. The signal was amplified using a custom-made amplifier and recorded through the audio input of a Sony TR7000 Digital 8 Handicam while videotaping the caterpillars. Videoclips were imported to a Power Mac (G3) by fire-wire as Imovie files, and sections of interest were saved as Quicktime Pro files. Vibration signals were subsequently extracted and converted to aiff files, and analyzed using Canary Bioacoustics Research Program (Charif *et al.*, 1995). Signal measurements presented in the results section were taken from 12 video clips of different resident caterpillars that were prompted to signal by introducing a conspecific to their shelter.

Behavioral Trials

To examine the context of signaling and the stimuli that evoke signaling, we conducted two sets of behavioral experiments. The first involved a staged encounter between a resident larva (actively spinning/rolling a leaf) and an introduced larva (intruder). The behavior of the resident was recorded 2 min prior to the introduction of the intruding larva to provide a baseline for comparison. If larvae use signals for conspecific communication such as territorial encounters, we predicted that signals would be produced at a higher frequency in the presence of a conspecific than when alone. We also predicted that the presence of a conspecific, and not just mechanical disturbance to the shelter, would be necessary to elicit a signaling response. To test this, we conducted a second experiment that involved mimicking the mechanical disturbance created when placing a second larva on the shelter with a fine paintbrush. The paintbrush lightly touched the interior of the shelter and we recorded the resident's behavior two minutes prior to (control period) and 2 min following the disturbance.

For each type of trial, we selected completed leaf rolls from the black cherry cuttings (10 for the staged encounters and 11 for the paintbrush disturbance), unrolled the shelter and allowed the resident to start building a new shelter on either a fresh or the original leaf. Trials did not begin until the caterpillar had resumed building (i.e. spinning) for at least 5 min. A ceramic phonocartridge was placed in contact with the underside of the leaf to record any substrate vibrations produced by the caterpillar, and a Sony Digital8 TR7000 camcorder recorded all of the events during the experiments. As a control, we filmed the behavior of the resident caterpillar for 2 min before introducing the disturbance (conspecific or paintbrush); once introduced, the trial lasted for 2 min. Ten staged encounters with a resident and intruder took place although only seven of these could be used for pairwise comparisons since in three trials one of the larvae was not visible for $\geq$50% of the trial. A total of 17 caterpillars were used in the conspecific trials, indicating that three caterpillars were used twice. Trials were spaced sufficiently apart however (by at least 1 day), to ensure that this did not interfere with the outcome of the encounters. The paintbrush trials involved 11 additional caterpillars.

Statistical Analyses

To analyze the two experiments, we divided the caterpillar's behavior into nine categories: biting (which included eating and weakening the leaf for rolling), scraping with mandibles, searching (lifting head and thorax off of the leaf), plucking with mandibles, walking, resting (no movement), spinning, vibrating (sitting in one place while body is shaking), and no data (caterpillar was out of view). Quantifying these behaviors took place by recording the presence or absence of each behavior in the resident (and intruder when applicable) within each consecutive 5 s interval for the control periods (prior to encounter and prior to paintbrush disturbance), staged encounters, and the paintbrush disturbance trials. This method provided an estimate of the time allocated to the nine behavioral categories under varying circumstances. To examine the frequency in which behaviors were exhibited under each circumstance, we tallied the number of 5 s blocks (5SB) in which a given behavior was recorded during a trial (i.e. the number of 5SB in which a resident exhibited scraping behavior after the introduction of an intruder). The number of 5SB could then be used in overall comparisons (i.e. all residents versus all intruders) or in pairwise comparisons (by individual trial). Overall comparisons were used for visually depicting trends in the figures (see Figs. 6–9) while the pairwise comparisons were used for statistical analyses.

The Wilcoxon Signed Rank Test was used for all pairwise comparisons. For the staged encounters, we compared the number of 5SB the resident spent in each behavioral category during the control versus experimental period to look for effects of introducing a conspecific to the shelter. We also looked for differences in behavior (allocation of 5SB) between the resident and intruder during the experimental trial. To look for effects of mechanical disturbance on behavior in the paintbrush experiment, we again compared the number of 5SB the resident spent in each behavioral category during the control and experimental period (pre- and post-disturbance, respectively).

To examine differences in behavioral time allocation of resident larvae when presented with a conspecific (staged encounter experiment) versus when subjected to mechanical disturbance (paintbrush experiment), we used the Mann–Whitney Test since this is not a paired comparison.

RESULTS

General Observations

Throughout the study, we opened approximately 70 leaf shelters. A single larva resided within the shelter in all but three cases and in these instances, the shelter contained two larvae at opposite ends of the enclosure. Therefore, larvae appear to generally live separately but occasionally have contact with other individuals. Encounters with other larvae may occur in the shelter-building process either while spinning or patrolling the leaf and, in several observed instances, have resulted in bouts of signaling between the individuals.

Sound Production

Distinguishing Behaviors

Scraping, plucking, and vibrations do not produce airborne signals perceivable by humans and thus require a phonocartridge (dubbed, piezoelectric sensor) to record and detect the substrate vibrations. Visually depicting the signals with an oscillogram allows one to find and measure temporal components such as the signal’s duration, time intervals between successive bouts of signaling, and the number of strokes per signal (for scrapes). These

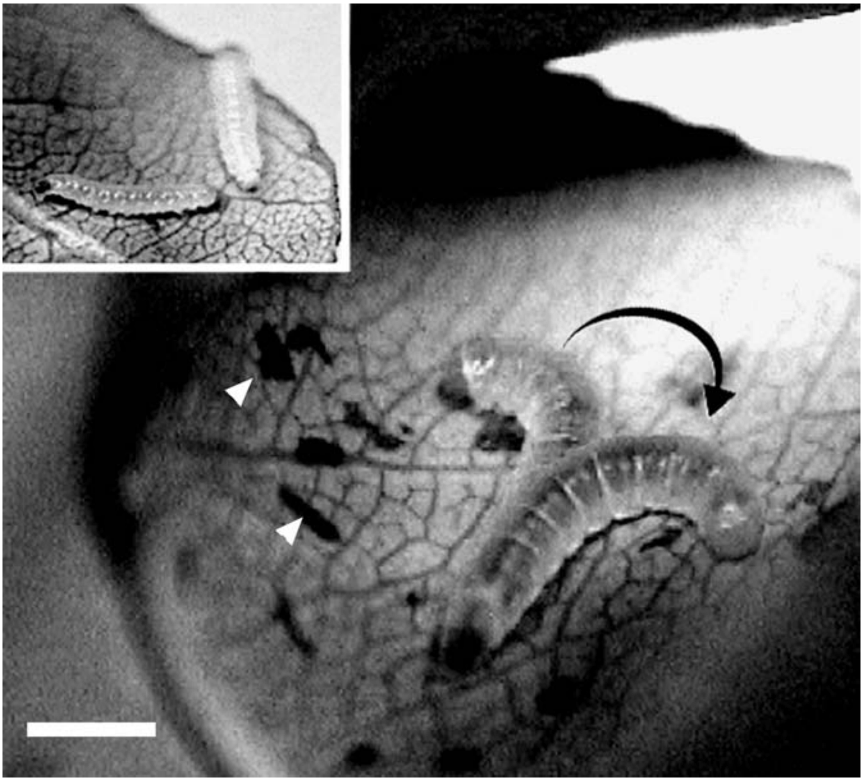

Fig. 2. Superimposed images of a video clip illustrating the final head swipe of a mandibular scraping event. White arrowheads point to feeding scars on the leaf surface. Scale bar: 2 mm. *Inset*: A resident shelter builder (*left*) and intruder engaged in a 'tête à tête' encounter, during which time both were producing scraping signals.

components provide a quantitative description of the sounds and highlight distinct patterns. With these measurements as well as visual information, the three signals were easily distinguishable from the other behaviors. The other behaviors (spinning, walking, biting, searching, and resting), with the exception of biting, were not normally detected by the phonocartridge and therefore, could not be mistakenly identified as a signal. Biting (which includes both feeding and biting the midrib) was detectable but easily distinguished from the other three signals by differences in temporal patterns (seen on oscillograms), and visual behavioral cues (seen on videotapes). The vibrational signals—scraping, plucking, and body vibrations—produce distinct visual and acoustic patterns, allowing for accurate identification between the three categories.

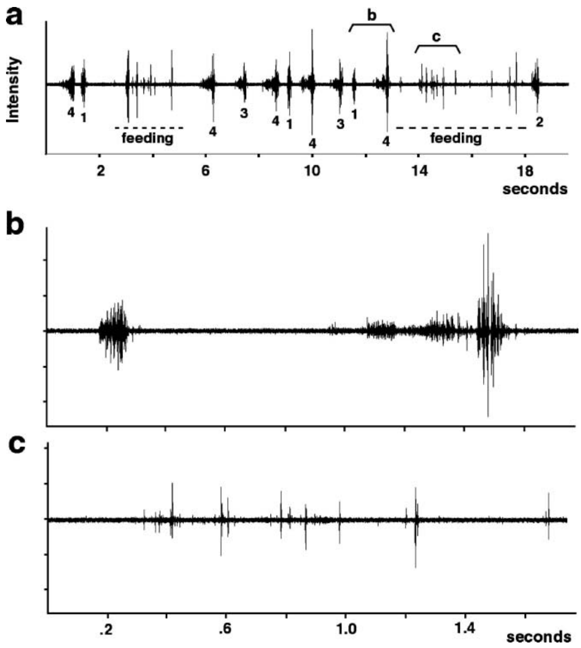

Fig. 3. Substrate-borne acoustic signals by a resident *C. serotinella* recorded with a piezoelectric sensor. (a) Oscillogram shows several mandibular scraping events interrupted by two short bouts of feeding (*underscored by broken lines*). Numbers below each scraping event indicate the number of mandibular 'swipes' occurring during that single event. Segments marked 'b' and 'c' are enlarged below. (b) Two scraping events expanded from the above oscillogram, with one and four head swipes (*left and right*, respectively) per event. Events with multiple head swipes, as shown in the right of the trace, show a gradual increase in intensity from the first to the last swipe. (c) Vibrations caused by individual bites of the leaf during feeding. Amplitude scales in b and c are equivalent.

Characteristics of the Signals and Means of Sound Production

Scraping. The scraping behavior involves pronounced lateral movements of the head and anterior thorax, while opened mandibles are scraped against the leaf surface (Fig. 2). Of the three signals, it is the most frequently used by the larvae during our experimental trials (see context section below and Fig. 8). Also, when scraping occurred adjacent to other behaviors, like feeding (Fig. 3), plucking (Fig. 4) and vibrating, scraping behavior consistently exhibited a higher overall amplitude. A single scraping event may

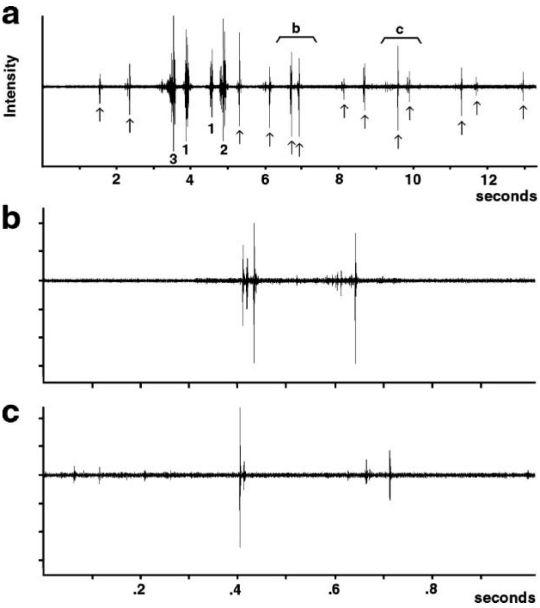

Fig. 4. Piezoelectric recording of a series of plucks and mandible scrapes. (a) Oscillogram shows a train of four scraping events (numbers beneath each event indicate the number of head swipes) flanked by several plucks (*arrows*). Segments marked ‘b’ and ‘c’ are enlarged below. (b and c) A total of four plucks expanded from the above oscillogram. The *y*-axis represents relative intensity and is equivalent in both traces, allowing for direct comparisons. Each plucking event typically contains one larger component (suggested to be a mandibular pluck) flanked by smaller components that may be caused by scratching of the legs or other body parts against the leaf surface.

encompass from 1 to 5 sequential mandible swipes, with an average of 3.3 swipes per event (SD 2.04, 64 events from 11 individuals) and an average duration of 386.65 ms (Sd 286.86, 57 events from 9 individuals) (see Table I for a summary of signal parameters). In general, the last swipe in a multi-swipe scraping event has the highest amplitude and moves the mandibles across the greatest distance over the leaf surface (Fig. 3b). Scraping events typically occur in trains (a sequence of scraping events only interrupted by short rests) lasting 3.65 s (SD 4.01, 11 trains from six individuals), with an average time interval between successive scraping events of 744.43 ms (SD 771.56, 26 intervals from six individuals). Figure 3a depicts a train of eight scraping events flanked on either side by feeding.

Table I. Comparison of Signal Parameters for Scrapes, Plucks, and Vibrations

	Duration of signal trains[a] (s)	Interval betw. signal trains (s)	Signal events/ train	Duration of signal event (ms)	Interval betw. signal events (ms)	Lateral head swipes per scrape event
Scrapes						
Mean	3.65	3.38	3.37	386.65	744.43	3.3
SD	±4.01	±1.87	±2.91	±286.86	±771.56	±2.04
n_1, n_2	11, 6	9, 5	19, 11	57, 9	26, 6	64, 11
Plucks						
Mean	4.07	3.58	6.27	41.64	488.95	
SD	±2.58	±2.57	±5.44	±24.44	±451.95	
n_1, n_2	8, 7	5, 2	15, 8	57, 6	33, 5	
						Vibrat. cycles[b] (s)
Vibrations						
Mean	23.87		2.6	2417.33		9.62
SD	n/a		±1.82	±2339.55		±1.52
n_1, n_2	1, 1		5, 5	12, 4		13, 5

n_1: Number of signals analyzed; n_2: number of individuals contributing signals.

[a] A train is defined as a sequence of signal events flanked on either end by a different behavior. If a signal was separated from others by a short rest, then it was still considered part of the sequence or train.

[b] A vibration cycle is one back and forth movement of the anterior part of the body.

Plucking. Plucking involves a simple vertical movement of the head and anterior end of the thorax. A signal is produced with each upward movement (Fig. 4), suggesting that either the mandibles or thoracic legs cause the signal by pulling up on the leaf. Careful observation of video recordings suggests mandibular involvement since the mandibles were consistently open as the head was lifted after a pluck. Individual plucks have a much shorter duration than scrapes, with an average time of 41.64 ms (SD 24.44, 57 events from six individuals); however, trains of plucks have a similar duration to those of scrapes at 4.07 s (SD 2.58, eight trains from seven individuals; see Table I). Plucking was clearly distinguishable from feeding due to differences in the temporal patterns (Figs. 3 and 4) and obvious differences in the two behaviors as observed on the video. Additionally, when feeding, larvae keep their heads close to the substrate and produce patches of skeletonized leaf (Fig. 2), which differs markedly from the quick upward movements associated with plucking behavior. Individual plucking events appear to be composed of one large amplitude component and several smaller components of variable amplitude (Fig. 4). Since each plucking event involves a single upward movement, we surmise that the largest component represents the mandibular pluck, while the smaller components are caused by the legs or other body

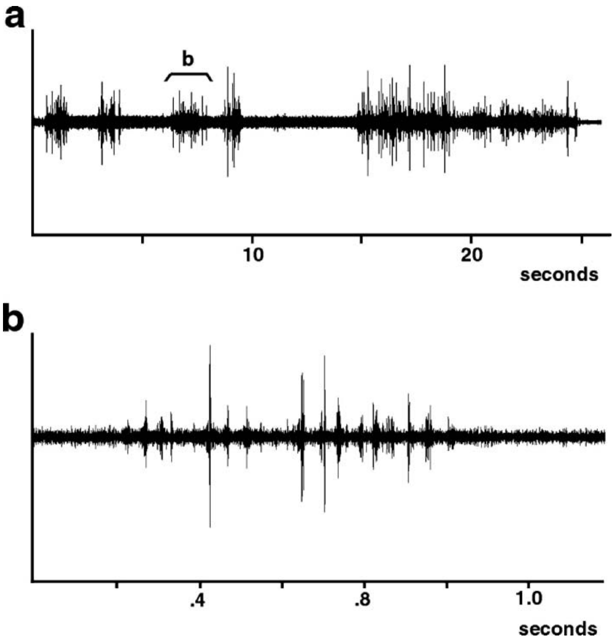

Fig. 5. (a) Oscillogram depicting a series of vibratory signals. (b) Enlargement of a single vibratory ‘bout’. The regular spike pattern depicts the small, rapid oscillatory movements of the anterior end of the body.

parts scratching the leaf, or they may simply be an artifact of the leaf resonating.

Vibrating. The least frequently observed signal was the vibratory signal (Fig. 5), comprising only 7% of the signaling behavior in the conspecific disturbance trials (Fig. 8). The caterpillar remains with its head and abdomen in a fixed position on the substrate leaf (although this was also observed once while an individual rested on the webbing of its shelter), and vibrates the thorax horizontally at a fairly regular rate of 9.62 (SD 1.52, 13 vibration events from five individuals) full oscillations per second. The average duration of a single vibration event at 2417.33 ms (12 events from four individuals) is much longer than that of a pluck or scrape but it also has a high variability (SD 2339.55), perhaps due to the low sample size. Trains of vibrations may also be longer than those of scrapes or plucks but with only one recording of an entire train, it is difficult to make comparisons. Although we could not determine the exact source of the vibration production, it appeared that the thoracic legs were being scraped against the substrate.

Context of Signaling—Behavioral Trials

Staged Interactions with Conspecifics

In each of these trials, after a 2-min control period of observing the resident's behavior, a conspecific caterpillar was lowered via a paintbrush into the shelter of an actively building larva. We recorded the behavior of the intruder and resident at 5-s intervals for 2 min. For residents, time observed (number of 5SBs) in three of the behavioral categories differed significantly between the control and experimental period (see Fig. 6). Resident larvae scraped significantly more and spun significantly less when in the presence of a conspecific than when alone (Wilcoxon signed rank test, $n = 7, p = 0.035$ for both). They also exhibited biting behavior significantly less when in the presence of an intruder than during the control periods (Wilcoxon signed rank test, $n = 7, p = 0.05$). The behavior of residents and intruders differed in that residents initiated signaling (scraping) events more often than intruders (eight out of 10 trials). Additionally, residents scraped significantly more than intruders during a trial (Wilcoxon signed rank test, $n = 7, p = 0.035$; see Fig. 7).

Larvae exhibited all three signals during the experimental trials; however, their frequency of use varied greatly. During the 10 2-min trials, signaling by either the resident or intruder occurred in 152 of the 446 possible 5SB (229 for resident, 217 for intruder—note—numbers differ since in three cases larvae were not visible for the entire trial). The majority of the signaling involved scraping (83%), followed by plucking (11%), and then vibrating (7%) (Fig. 8). Correspondingly, a total of 12 individuals exhibited scraping behavior, three exhibited plucking, and only one individual vibrated during the trials. Of the plucking signals, two occurred amidst bouts of scraping and the third occurred prior to the onset of vibrating, suggesting that plucks are used in association with other signals. We never recorded scraping and vibrating occurring together and noticed that they may differ in their context of use. Scraping occurred when larvae were in relatively close proximity to each other, while in the observed cases of vibrating, larvae were further apart from each other on the leaf.

Scraping briefly occurred only twice and plucking once (in association with one of the scrapes) in the 10 control periods prior to the introduction of a conspecific. In each case, they took place during bouts of biting behavior.

Control: Disturbance with Paintbrush

As a control for general disturbance during the introduction of a conspecific, 11 caterpillars were disturbed with a paintbrush. We scraped

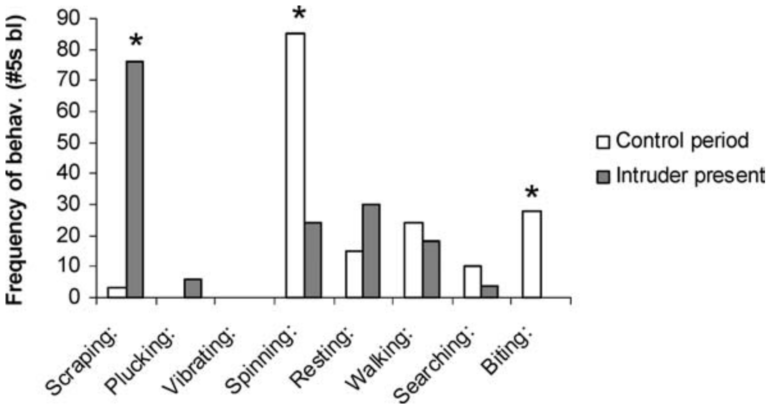

Fig. 6. Comparison of the behavior of resident larvae during the control period (*white bars*) and after the introduction of a conspecific intruder (*gray bars*). The y-axis (for Figs. 6–9) is the total number of 5-s blocks in which a given behavior was recorded (combining all trials used in the analysis). Residents were observed to be scraping significantly more and spinning and biting less when in the presence of a conspecific than when alone. Asterisks indicate significant differences in the residents' behavior between control periods and encounters with conspecifics (Wilcoxon signed rank test, $n = 7$, $p = 0.035$ (scraping, spinning), $p = 0.05$ (biting)).

the paintbrush inside the shelter and recorded the resident's behavior for 2 min. Only nine trials were used in the analysis since two of them had unreliable acoustic recordings (due to the phonocartridge losing contact with the leaf during a trial) which are necessary to validate visual behavioral observations. Comparisons of the residents' behavior before and after the disturbance revealed significant differences in the observed time spent spinning and resting. Larvae were observed spinning significantly less and resting significantly more after the disturbance than during the control periods (Wilcoxon signed rank test, $n = 9$, $p = 0.018$ and $p = 0.022$, respectively; see Fig. 9). No signaling occurred during the control periods and only one brief bout of scraping occurred in the experimental trials after a larva was accidentally touched by the paintbrush.

Comparing the effect of different disturbances (mechanical via paintbrush versus a conspecific) on the behavior of resident larvae revealed a significant difference only in the observed time spent scraping. Residents in the staged encounter trials scraped significantly more than residents disturbed by a paintbrush (Mann–Whitney test, $n = 18$, $p = 0.0006$). Caterpillars from both treatments increased the amount of time spent resting after their respective disturbances.

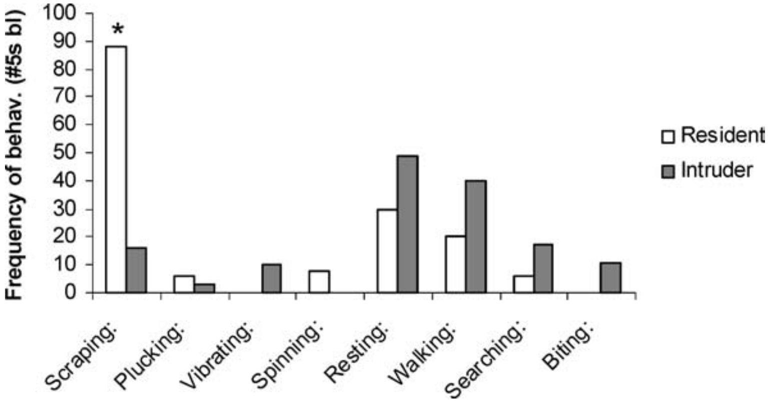

Fig. 7. Behavioral comparison of resident (*white bar*) and intruder (*gray bar*) larvae during the 2-minute encounter trials. Residents were observed scraping significantly more during a trial than intruders (Wilcoxon's signed rank test, $n = 7$, $p = 0.035$). None of the other behaviors were significantly different between residents and intruders.

DISCUSSION

This study provides a first step toward understanding the role that vibrational signaling plays in the communication system of the cherry leaf

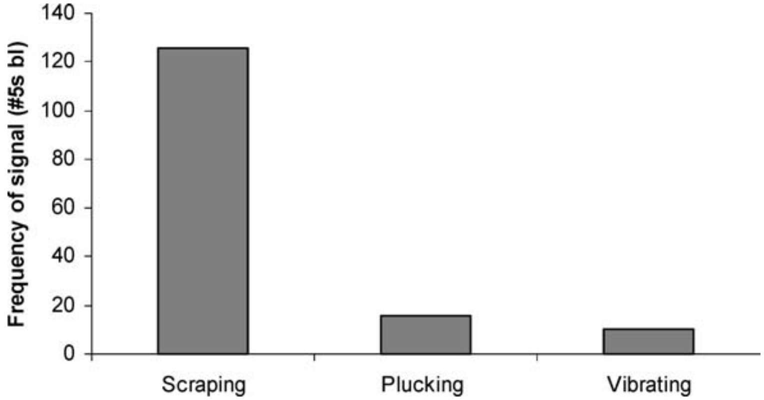

Fig. 8. Frequency of signal use by *C. serotinella* larvae. During the staged encounter trials, signaling behavior was observed for a total of 152 5SB. Eighty-three percent of that time was spent scraping, 11% was spent plucking, and 7% was spent vibrating.

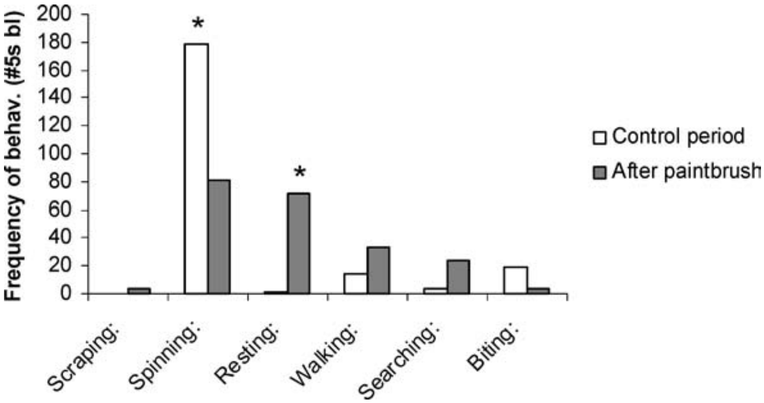

Fig. 9. Comparison of larval behavior before and after mechanical disturbance to the shelter by a paintbrush. Asterisks indicate significant differences in spinning and resting behavior between the control and disturbance periods (Wilcoxon signed rank test, $n = 9$, $p = 0.018$ (spinning) and $p = 0.022$ (resting)). Larvae were observed spinning significantly less and resting significantly more after the disturbance than during the control period.

roller caterpillar, *C. serotinella*. We have established that late instar larvae produce three substrate-borne vibrational signals, scraping, vibrating and plucking, that are distinct from each other as well as from other common behaviors such as walking, spinning, and feeding. Spinning does not induce any detectable vibrations and although feeding does, it is easily distinguishable from the signals when video and acoustic analyses occur simultaneously.

The function of the signals is strongly associated with conspecific interactions, and resembles other reported examples of vibrationally-mediated territorial encounters in other larval insects (see below). In *C. serotinella*, signaling is primarily initiated and produced by the resident during conspecific encounters. Our experimental results show that residents signaled significantly more when an intruder was present than during the pre-trial control period (on average only 2.1% of the time during control periods and 48.1% of the time during experimental encounters). Although none of the residents exhibited vibrating behavior during the experimental trials, other video recordings of encounters used for signal analysis did show residents utilizing the signal. Therefore, when including all behavioral observations, both residents and intruders were observed to perform each of the three signaling behaviors. Scraping was by far the most frequently used signal observed and residents scraped significantly more than the intruders during encounters. No significant differences were observed between the amounts of plucking and vibrating produced by residents and intruders, although this would likely be clarified with larger sample sizes, and/or staging experiments under more natural conditions (see discussion below).

While the presence of a conspecific clearly elicited signaling behavior in residents, especially scraping, other forms of disturbance generally failed to evoke these behaviors. When resident larvae were mechanically disturbed with a paintbrush in our control experiment, they typically decreased web spinning behavior and remained still, but did not significantly increase signaling. Other possible functions for signaling were explored briefly by staging some encounters with heterospecific caterpillars as well as predators such as wasps and jumping spiders. In all cases, no signaling was observed. It is unlikely that signaling would provide any protection against vertebrate predators, since the signals produced by *C. serotinella* are not audible. Although additional trials are needed to clarify the patterns of signaling made by both residents and intruders during conspecific encounters, and what other specific kinds of stimuli might evoke signaling behavior, our evidence for the association of signaling and the presence of another conspecific caterpillar is strong.

The signaling behavior of *C. seritonella* is reminiscent of a few other reported examples of vibrationally-mediated territorial behaviors in larval insects. The hooktip moth larva *D. arcuata*, produces three distinct signals (mandible drumming, scraping, and anal scraping) during ritualized territorial encounters over silken leaf shelters (Yack *et al.*, 2001). As a conspecific intruder approaches a resident caterpillar in its leaf shelter, the signaling pattern of the resident escalates in the rate, kind, and overall amplitude. For example, mandible scraping, the loudest of the three signals, occurs most often when the intruder is inside the resident's nest, while anal scraping occurs near the beginning of an encounter and increases in rate as the intruder approaches. The functional significance of the three signals produced by *C. serotinella* is perhaps similar to that observed for *D. arcuata*. In staged encounters, there was clearly variability in the amounts of the different signals produced (e.g. mandible scraping was most frequent, followed by plucking, and then vibrating), and the rate and duration of individual signals (e.g. a scraping event could comprise from 1 to 5 consecutive head swipes) or trains of signals. We also noticed that scraping, the loudest of the signals, tends to occur when the two individuals are very close together, while the few cases of vibrating occurred when the larvae were further apart. One of the logistical problems with our study, unlike for that of *Drepana* which lives in open leaf shelters and can be easily viewed without disturbance, was that we had to unroll the leaf shelters in order to observe the larvae. This may have altered the normal pattern of signaling that may be observed under more natural conditions whereby an intruder would gradually approach and enter an enclosed leaf roll, rather than being placed directly in the roll, near the resident. This problem is difficult to overcome, but perhaps recording with a more sensitive recording device, such as a laser vibrometer, would allow for non-invasive recordings of the vibrations produced in enclosed nests. Other factors that might influence the motivation and/or ability to defend a leaf shelter include larval size, leaf quality, and time invested in shelter construction. The influence of such factors on signal patterns should be investigated in future studies.

In addition to *D. arcuata* and *C. serotinella*, at least two other species of larval Lepidoptera, *Diurnea fagella* (Oecophoridae) (Hunter, 1987) and *Sparganothis pilleriana* (Tortricidae) (Russ, 1969), and several species of larval Trichoptera (Jansson and Vuoristo, 1979) have been reported to engage in vibrationally-mediated territorial encounters. In all of these cases, including that of *C. serotinella* reported here, the larvae occupy shelters, which are typically expensive to build and valuable to own. Ritualized fighting in the form of acoustic signaling might allow contestants to advertise ownership, assess one another's size, and resolve most conflicts without physical fighting and injury that could lead to death (e.g. Weyh and Maschwitz, 1982; Okuda, 1989; Berenbaum *et al.*, 1993). Considering that there are many species of larval Lepidoptera occupying leaf shelters at some stage of their development (e.g. Cappuccino, 1993; Rose and Lindquist, 1997; Nakamura and Ohgushi, 2004), and that vibrational signals are typically not audible to humans, the phenomenon of vibrational communication for the purposes of spacing and territorial defense may indeed be widespread, and requires further investigation.

ACKNOWLEDGMENTS

We thank A.M. Jose for assistance with data analysis, and two anonymous reviewers for their helpful comments on the manuscript. Funding to support this project was received from a NSF Predoctoral Fellowship to LEF, a NIDCD of the NIH to RRH, and a NSERC of Canada to JEY.

REFERENCES

Berenbaum, M. R., Green, E. S., and Zangerl, A. R. (1993). Web costs and web defense in the parsnip webworm (Lepidoptera: Oecophoridae). *Environ. Entomol.* **22:** 791–795.

Cappuccino, N. (1993). Mutual use of leaf-shelters by lepidopteran larvae on paper birch. *Ecol. Entomol.* **18:** 287–292.

Charif, R. A., Mitchell, S., and Clark, C. W. (1995). *Canary 1.2 User's Manual*, Cornell Laboratory of Ornithology, Ithaca, New York.

Cocroft, R. B. (2001). Vibrational communication and the ecology of group-living, herbivorous insects. *Amer. Zool.* **41:** 1215–1221.

Cocroft, R. B., and Rodríguèz, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience* **55:**323–334.

Costa, J. T., and Pierce, N. E. (1997). Social evolution in the Lepidoptera: Ecological context and communication in larval societies. In Choe, J. C., and Crespi, B. J. (eds.), *Social Behavior in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 407–442.

Fitzgerald, T. D. (1995). Caterpillars roll their own. *Nat. Hist.* **104:** 30–37.

Fitzgerald, T. D. (2003). The role of a trail pheromone in the foraging and processionary behavior of *Thaumetopoea pityocampa*. *J. Chem. Ecol.* **12:** 513–532.

Fitzgerald, T. D., and Clark, K. L. (1994). Analysis of leaf-rolling behavior of *Caloptilia serotinella* (Lepidoptera: Gracillariidae). *J. Insect Behav*. **7:** 859–872.

Fitzgerald, T. D., Clark, K., Vanderpool, R., and Phillips, C. (1991). Leaf shelter-building caterpillars harness forces generated by axial retraction of stretched and wetted silk. *J. Insect Behav*. **4:** 21–32.

Fitzgerald, T. D., and Costa, J. T. (1999). Collective behavior in social caterpillars, In Detrain, C., Deneubourg, J. L., and Pasteels, J. M. (eds.), *Information Processing in Social Insects*. Birkhauser, Basel, pp. 379–400.

Hallberg, E., and Poppy, G. (2003). Exocrine glands: Chemical communication and chemical defense. In Kristensen, N. P. (ed.), *Handbook of Zoology*: Vol. IV Arthropoda: Insecta. Part 36. Lepidoptera, Moths and Butterflies, vol. 2, W. G. De Gruyter, New York, pp. 361–375.

Hunter, M. D. (1987). Sound production in larvae of *Diurnea fagella* (Lepidoptera: Oecophoridae). *Ecol. Ent.* **12:** 355–357.

Jansson, A., and Vuoristo, T. (1979). Significance of stridulation in larval Hydropsychidae (Trichoptera). *Behaviour* **71:** 167–186.

Minet, J., and Surlykke, A. (2003). Auditory and sound producing organs. In Kristensen, N. P. (ed.), *Handbook of Zoology*: Vol. IV Arthropoda: Insecta. Part 36. Lepidoptera, Moths and Butterflies, vol. 2, W. G. de Gruyter, New York, pp. 289–323.

Nakamura, M., and Ohgushi, T. (2004). Species composition and life histories of shelter-building caterpillars on *Salix miyabeana*. *Entomol. Sci.* **7:** 99–104.

Okuda, T. (1989). Aggressive characteristics of diapausing larvae of a Stem Borer, *Busseola fusca* Fuller (Lepidoptera: Noctuidae) in artificially crowded conditions. *Appl. Ent. Zool.* **24:** 238–239.

Poirier, L. M., and Borden, J. H. (1995). Oral exudate as a mediator of behavior in larval Eastern and Western Spruce Budworms (Lepidoptera: Tortricidae). *J. Insect Behav*. **8:** 801–811.

Rose, A. H., and Lindquist, O. H. (1997). *Insects of eastern hardwood trees*. Natural Resources Canada. Forest Technical Report 29.

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

Russ, K. (1969). Beiträge zum Territorialverhalten der Raupen des Springwurmwicklers, *Sparganothis pilleriana* Schiff (Lepidoptera: Tortricidae). *Pflanzenschutz Ber. Wein*. **40:** 1–9.

Virant-Doberlet, M., and Cokl, A. (2004). Vibrational communication in insects. *Neotrop. Entomol.* **33:** 121–134.

Warrant, E., Kelber, A., and Kristensen, N. P. (2003). Eyes and vision. In Kristensen, N. P. (ed.), *Handbook of Zoology*: Vol. IV Arthropoda: Insecta. Part 36. Lepidoptera, Moths and Butterflies, vol. 2, W. G. de Gruyter, New York, pp. 325–359.

Weyh, R., and Maschwitz, U. (1982). Individual trail marking by larvae of the scarce swallowtail *Iphiclides podalirius* L. (Lepidoptera; Papilionidae). *Oecologia* **52:** 415–416.

Yack, J. E., Smith, M. L., and Weatherhead, P. J. (2001). Caterpillar talk: Acoustically mediated territoriality in larval Lepidoptera. *P.N.A.S.* **98:** 11371–11375.