Context-Dependent Stridulatory Responses of *Leptogenys kitteli* (Hymenoptera: Formicidae) to Social, Prey, and Disturbance Stimuli

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ABSTRACT Individual *Leptogenys kitteli* (Hymenoptera: Formicidae) workers produce stridulatory pulses at faster rates after exposure to prey larvae placed nearby the nest and after air-puff disturbances at the nest entrance than during unstimulated social interactions within the nest. Workers produce chirps (trains of stridulatory pulses) at faster rates after exposure to prey larvae than during unstimulated social interactions, including groups of chirps (bursts) where the intervals between chirps decrease below 60 ms. Such bursts do not occur in unstimulated social interactions. Chirp bursts with intervals <10 ms (disturbance bursts) occur immediately after air puffs at the nest entrance. Disturbance bursts are not observed after exposure to prey larvae or during unstimulated social interactions. The rates of disturbance bursts decline rapidly within 10 s after an air puff, whereas episodes of chirp bursts extend over periods of 30 s or longer when groups of ants are moving prey larvae into the nest. The differences in the rates of stridulatory pulses and chirps and in the durations of stridulatory activity observed in the context of different types, intensities, and durations of stimulation contribute to evidence that stridulation has a significant communicatory role in colony activities of many ant species, even in genera, such as *Leptogenys*, in which a stridulatory organ has not been retained in every species. A better understanding of how ants produce and interpret vibrations may lead to new methods that to improve attractiveness of baits, or repel ants from electrical equipment housings where opportunistic colonies frequently nest.

KEY WORDS Ponerinae, communication, behavior, evolution

Leptogenys kitteli (Mayr) (Hymenoptera: Formicidae) is a species of commonly observed but little-studied army ants that hunt in groups in broadleaf and coniferous forests in lowland and hilly areas of Taiwan. These ants live in soil or litter and move their nests frequently. Like many other formicids, *L. kitteli* has a band of ridges on the gaster and a scraper on the postpetiole that is used as a stridulatory organ (Markl 1965, Spangler 1967). The functions of stridulatory organs in ants are not fully established but, in many species, stridulation behaviors play a role in movement of soil particles during excavation (Spangler 1974, Rauth and Vinson 2006) or leaf-cutting activities (Tautz et al. 1995) and in the rescue of trapped or buried nestmates (Markl 1965). Stridulations have been observed in several species during food retrieval behaviors (Markl and Hölldobler 1978), trophallaxis, allogrooming, and brood manipulation behaviors (Stuart and Bell 1980), and during alarm communi-

cation behaviors after disturbances (Roces and Hölldobler 1995). *Leptogenys* is a member of the Ponerinae, many species of which are nomadic, and several of which lack a stridulatory organ (Markl 1973). The presence of stridulatory organs in some but not all members of this genus is of particular relevance for studies of the evolution of ant stridulatory communication (Markl 1973).

L. kitteli are known to stridulate while handling prey (Y.-K.C., unpublished data), but until now their stridulatory behaviors have not been studied in detail. A laboratory study was conducted to measure the temporal and spectral characteristics of stridulations in response to different excitatory stimuli in behavioral interactions among workers. The results of the study suggested also the consideration of more general contexts, for example, where vibrational signals might be incorporated into control methods against pest ant species.

Materials and Methods

Insects and Recording Procedures. Six *L. kitteli* nests containing ≈400 workers each were collected from colonies in wooded areas in Nantou County near Taichung, Taiwan. Each nest was placed inside an acrylic petri dish with a small opening for worker entry and exit, and kept in a 22-cm-diameter by 6.5-cm-tall

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cylindrical acrylic arena containing a base layer of moistened gypsum. A red acrylic plate was placed over the petri dish to reduce disturbance. Moistened cotton provided a water supply and *Tenebrio molitor* L. larvae were provided as food. No queens were present initially, but soon after the nests were collected, a few workers in each colony began to lay eggs, as has been observed in other ponerines (e.g., Trunzer et al. 1999). The colonies were maintained in an incubator on a photoperiod of 12:12 (L:D) h at 26°C and 70–80% RH. To conduct recordings, the arena was moved into a noise-shielded enclosure constructed from two layers of blanketing material, and the ants were allowed sufficient time to return to their normal activity levels before measurements began.

Workers produced stridulations in the arenas in response to various treatments, including 1) feeding or social interactions involving low-intensity activity with nestmates; 2) when a *T. molitor* larva was placed into the arena as a prey item, eliciting moderate activity by ants which moved the larva into the nest; and 3) immediately after an air puff was applied with a ≈30-ml sprayer at the opening of the nest. The air puff elicited an intense but brief, ≈10-s alarm response from all the ants near the opening, which died out rapidly in the absence of additional disturbance (see Results). These three types of stimuli were selected to encompass different aspects of colony life as well as different levels of central nervous system excitation (Dethier et al. 1965, van Staaden and Huber 2001). The six nests were exposed consecutively to each of these three treatments twice on two different days. Each treatment was separated by an acclimation period sufficient for the ants to return to a normal state. Signals were collected and recorded using a stereo microphone (model AT9842, Audio-Technica, Tokyo, Japan) placed a few cm above the nest, and an audio recorder (model MZ-NH700 Hi-MD, Sony, Tokyo, Japan). The digitization rate was 44.1 kHz. Background noise was assessed before testing each day by recording from a nestless arena. The ants were visually observed and the signals were monitored with headphones in real time as the microphone signals were recorded for ≥1-min periods. In general, visible up-and-down oscillations of a gaster (Markl and Hölldobler 1978, Cammaerts and Cammaerts 1998) corresponded with acoustic detections of stridulation. Approximate numbers of stridulating ants could be estimated visually when they were attending prey items in the arena, but not when they were inside the nest.

It should be noted that although the stridulations were recorded as air-transmitted signals, easily detected by readily available inexpensive acoustic systems, the ants themselves sensed the stridulations primarily as substrate vibrations (Roces and Tautz 2001). In other experiments where stridulations have been monitored by microphones and vibration-sensing accelerometers (e.g., Markl and Hölldobler 1978), the signals were comparable in temporal pattern and spectral range, as has been seen also for a variety of other insect-produced sounds (Mankin et al. 2010).

Signal Processing. The unfiltered signals (.wav files) were screened with Raven 1.3 (Charif et al. 2008) to establish their general characteristics. Significant levels of background noise <200 Hz obscured the weakest stridulations; consequently, a high-pass, 200-Hz filter was applied to all subsequent analyses where it was important to identify individual stridulatory pulses or trains of closely spaced pulses (chirps) (nomenclature as in Eliopoulos 2006). Spectrograms were calculated in Raven using 64-point (1.45 ms) time slices with 90% overlap. Measurements of chirp amplitudes and timing of chirp durations and intervals between chirps were performed with Raven or Audition 2.0 (Adobe Systems, San Jose, CA), by using a 4–15-kHz band-pass filter to facilitate chirp visualization. Measurements of intervals between stridulatory pulses within a chirp were performed using Raven.

Spectral comparisons of unfiltered chirps were conducted using a customized, insect sound processing program, DAVIS (Mankin et al. 2000, Mankin et al. 2008b). Analyses were performed on 512-point (11.6-ms) time slices, with spectrum levels relative to the maximum acceleration, A_{max}, between 0 and 20 kHz, i.e., dB = $20 \log_{10}(A/A_{max})$ (Mankin and Benshemesh 2006).

Statistical Analyses. Because the numbers and durations of chirps and the intervals between stridulatory pulses exhibited high variability and were not normally distributed, nonparametric, one-way repeated measures analyses of variance by rank, Friedman's tests (SAS Institute 2004), were conducted to compare chirp counts, chirp durations, and median stridulatory pulse intervals within chirps during unstimulated social interaction, prey, and air puff treatments of different nests. Where significant differences among responses to different treatments were found, nonparametric Wilcoxon signed rank tests (SAS Institute 2004) were performed on specific comparisons between prey and unstimulated treatments, prey and air puff treatments, and air puff and unstimulated treatments.

Results

General Characteristics of Stridulatory Pulses and Chirps. Brief, 25–95-ms chirps, random samples of which contained a range from 14 to 86 stridulatory pulses, were recorded from each of the six *L. kitteli* nests during at least two of the four prey larva and air puff treatments. During unstimulated treatments, chirps were detected in at least one record from each but one nest. A series of three chirps recorded over a 700-ms period during an unstimulated treatment is displayed at D-F in Fig. 1. The chirps in this example contained peak energies below one kHz and a secondary peak between 6 and 10 kHz (see rounded rectangles in D and F in Fig. 1B). Examples of individual stridulatory pulses in the train comprising the first chirp are shown in the inset (Fig. 1C).

The intervals between chirps in unstimulated and prey larva treatments were variable, because 1–5-s episodes of stridulation were separated by longer,
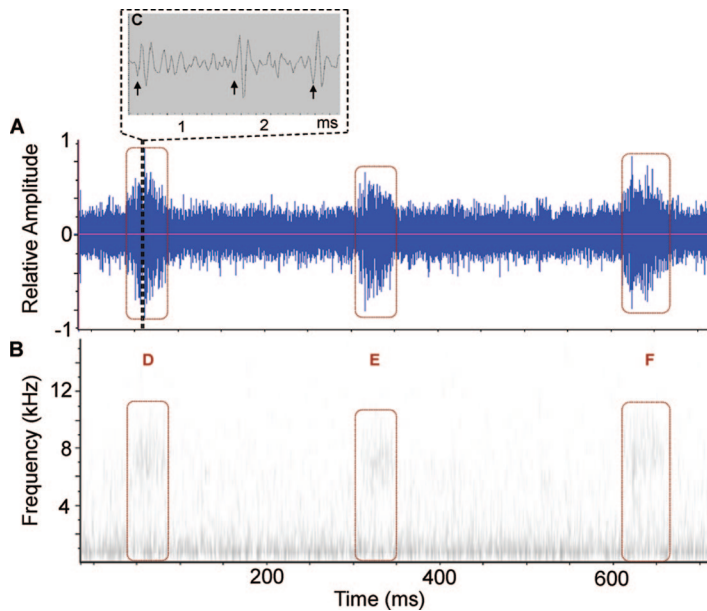
Fig. 1. Oscillogram (A) and spectrogram (B) of 700-ms period of stridulations recorded during an unstimulated treatment. Inset (C) in dashed rectangle expands a 3-ms period showing three stridulatory pulses (with beginnings marked by arrows) in the first of three chirps (marked by rounded rectangles D–F). Dashed lines mark the beginning and ending times of the inset. Darker shades in the spectrogram indicate higher relative spectrum level. Signals in A and C were band-pass filtered between 4 and 15 kHz for easier visualization. (Online figure in color.)

quiet periods. In stridulation episodes during unstimulated treatments, the intervals between chirps varied considerably but typically exceeded 100 ms. Chirp intervals noticeably decreased during prey larva treatment episodes, and bursts of chirps occurred frequently in which intervals between chirps were <60 ms, as in Fig. 2A (rectangle C). Because the temporal patterns of chirp bursts were different among treatments (see below), their time courses were tracked for subsequent analyses.

Multiple chirps separated by <10 ms intervals were observed immediately after each air puff treatment, as seen in the example of Fig. 3. The intervals between chirps within these bursts often were so short that chirps from different individuals overlapped, as in the inset, Fig. 3B with rounded rectangles, C and D, which contained pulses of uniform amplitude as in a typical chirp, but were not temporally separated from neighboring chirps as in Figs. 1 and 2. Because these bursts of short-interval chirps were observed consistently for
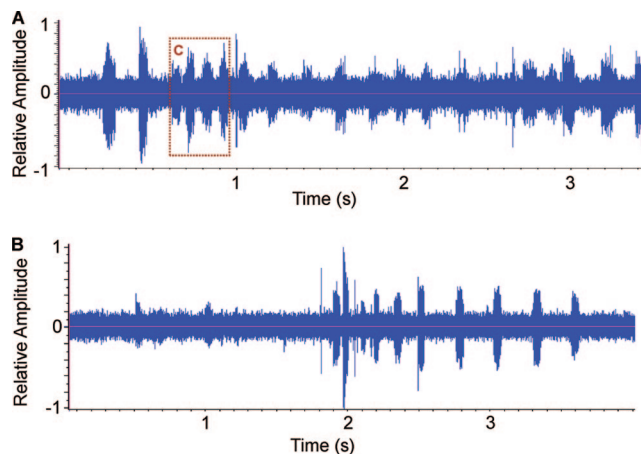

Fig. 2. Oscillogram of 3.5-s (A) and of 4-s (B) periods of stridulation showing chirps of various amplitudes and interchirp intervals recorded from two different *L. kitteli* nests exposed to prey larvae. A chirp burst containing intervals <60 ms between chirps is displayed inside dotted rectangle (C) in A. Signals in A and B were bandpass filtered between 4 and 15 kHz. (Online figure in color.)
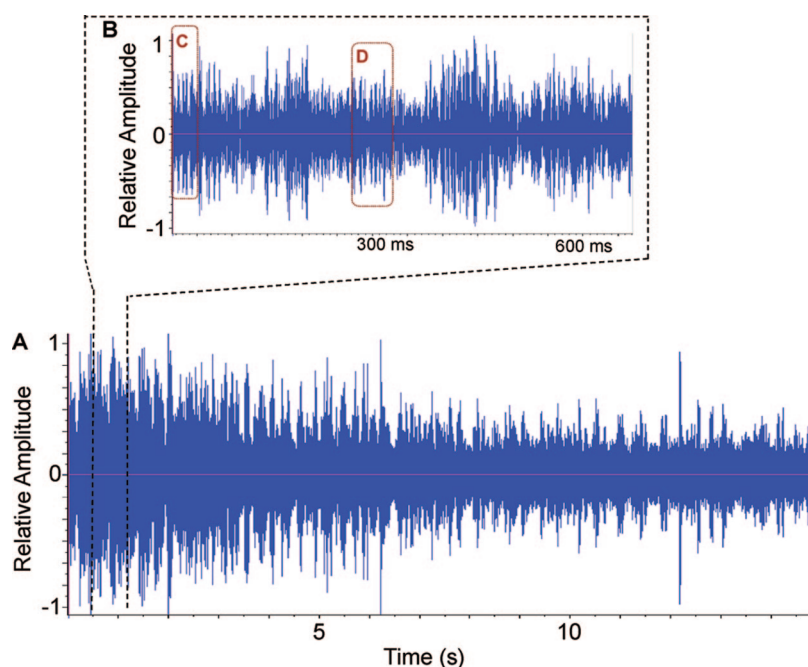
Fig. 3. Oscillogram (A) of stridulation chirps recorded in a 15-s interval immediately after air puff stimulus at nest entrance; inset (B) expands a 700-ms period recorded at 0.465 s. Rounded rectangles (C and D) mark two groups of pulses, each with relatively uniform pulse amplitudes, possibly indicative of signals from a single ant (see text). Signals were bandpass filtered between 4 and 15 kHz. (Online figure in color.)

≈10-s intervals each air puff disturbance and not at other times, we denoted them as disturbance bursts and tracked their time courses for subsequent analyses (see below).

Temporal Features of Chirp and Burst Patterns. The time courses of chirps, chirp bursts, and disturbance bursts had different patterns. Individual chirps were observed at irregular intervals during the entire 60-s recording period in all treatments. Chirp bursts were observed for ≈30 s after a prey larva or air puff treatment, but were never observed during an unstimulated treatment. After an initial 30-s period with high rates of bursts, episodes of chirp bursts continued in tests where the prey were delayed in being carried into the nest. Continued episodes of chirp bursts were not observed, however, after air puff treatments. Finally, disturbance bursts were observed only during air puff treatments, and their rates of occurrence decreased rapidly within 10 s after a puff, as in the example of Fig. 3A.

Numbers of Stridulating Ants in Different Treatments. The numbers of ants stridulating during different treatments were difficult to determine unambiguously, but order of magnitude estimates could be obtained by combining visual observations with analyses of chirp amplitude distributions. Visual observations suggested that two to eight workers were interacting simultaneously and had potential to be producing chirps during each of the different stridulation episodes that occurred while a prey larva was being moved from the arena into the nest. Many more,

perhaps 20–100 ants, interacted briefly during air puff treatments. In the unstimulated treatments, however, it was difficult to identify visually which ants might be stridulating during a recording.

Analyses of the treatment records provided complementary estimates about the numbers of ants producing chirps during the unstimulated and prey larva treatments. In the unstimulated and prey larva records, it was frequently observed that a series of chirps of relatively uniform amplitude were produced over 1–2-s periods, as in the examples of Figs. 1 and 2. Considering that only two to eight ants usually participated in moving a prey larva into the nest, the appearance of a series of chirps of one amplitude followed by a series of chirps of notably different amplitude, as in oscillograms A and B in Fig. 2, may indicate that two different ants had each separately produced a series of chirps. Other examples of the distributions of chirp amplitudes in unstimulated, prey larva, and air puff treatments are shown in Fig. 4. The distributions were not normally distributed, but rather were clumped in both the unstimulated and prey item treatments. In contrast, the distributions were more uniform in the air puff treatment. Examination of chirp amplitude distributions in other recordings not included in the figure revealed considerable variation but, as in Fig. 4, there were typically two to five peaks containing a high proportion of the chirp amplitudes in unstimulated and prey larva treatments, and less well defined peaks of chirp amplitudes in air puff treatments, which would be expected if multiple ants
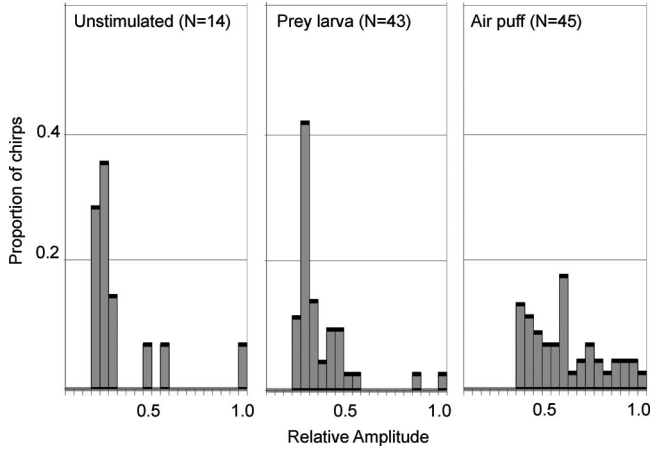
Fig. 4. Examples of chirp amplitude distributions in recordings from unstimulated, prey larva and air puff treatments. N indicates the number of chirps sampled.

with characteristically different chirp amplitudes were stridulating.

Considering the results of the visual observations and the chirp amplitude measurements together, we estimate then that the numbers of stridulating ants were approximately two to five for unstimulated treatments, two to eight for prey larva treatments, and 20–100 for air puff treatments.

Differences in Rates of Chirps, Chirp Bursts, and Disturbance Bursts Across Treatments. Comparing among treatments presented to the different nests, significant differences were found in chirp count rate (Friedman's test statistic = 7.91, df = 2, P = 0.02), chirp-burst count rate (Friedman's test statistic = 8.59, df = 2, P = 0.01), and disturbance burst count rate (Friedman's test statistic = 12, df = 2, P = 0.0025) (Table 1). The comparisons take into account the differences in the temporal patterns of chirps in unstimulated, prey larva, and air puff treatments by av-

eraging over periods when signals were most prevalent (see Temporal Features and Table 1).

Perhaps the most important result from Table 1 is that it enabled estimation of the ratio of the mean rate of chirps in prey larva treatments to the mean rate of chirps in unstimulated treatments, 1.714/0.106 = 16.2. Given that the numbers of ants stridulating in the unstimulated and prey larvae treatments were <10 ants (see Numbers of Stridulating Ants), the rate of chirps per individual ant increased ≈10-fold between the unstimulated and prey item treatment, i.e., the average rate of chirps per ant increased in response to a stimulus of greater excitatory intensity.

Spectral and Temporal Patterns of Stridulatory Pulses Within Chirps. The intervals between stridulatory pulses within chirps, the durations of chirps, and the overall spectral patterns of chirps produced in unstimulated, prey, and air-puff treatments were measured for assessment of the reactions to different stimuli. For these comparisons, chirps produced in each treatment were selected at random in one recording from each of the five nests where chirps were detected in an unstimulated treatment. In this case, chirps that occurred in chirp bursts and disturbance bursts were excluded because their beginnings and ends could not be distinguished easily. The median interval between stridulatory pulses within chirps was significantly different among treatments (Friedman's test statistic = 8.4, df = 2, P = 0.02; Table 2) and the range of intervals between pulses varied from 0.4 to two ms. Pairwise comparisons revealed that each of the exposure treatments differed from the unstimulated treatment, but the pulse intervals did not differ between the two exposure treatments. The mean chirp durations were not significantly different among the three treatments (Friedman's test statistic = 2.8, df = 2, P = 0.24).

The mean spectra of a randomly selected, 41-ms chirp from an air-puff treatment, a 31-ms chirp from a prey larva treatment, a 41-ms chirp from an unstimulated treatment, and a 100-ms section of background

Table 1. Means ± SE of rates of chirps, chirp bursts, and disturbance bursts in unstimulated, prey larva, and air puff treatments

Treatment	Chirps/s[a]	Chirp bursts/s[b]	Disturbance bursts/s[c]
Unstimulated	0.106 ± 0.048a	0a	0a
Prey larva	1.714 ± 0.625b	0.206 ± 0.094b	0a
Air puff	—[d]	—[d]	26.37 ± 6.78b

Means in a column followed by the same letter are not significantly different under Wilcoxon signed rank test.

[a] For unstimulated ranked with prey, t_s = 0, N = 6. P < 0.001. Rates were averaged over the 60-s recording period.

[b] For unstimulated ranked with prey, t_s = 0, N = 6. P < 0.001. Rates were averaged over the 30-s interval immediately after prey was placed in arena (see Temporal Features under Results).

[c] For unstimulated ranked with puff, t_s = 0, N = 6, P < 0.001; and prey ranked with puff, t_s = 0, N = 6, P < 0.001. Rates were averaged over the 10-s interval immediately following the air puff (see Temporal Features under Results).

[d] In air puff treatments, many chirps were merged together or were separated by intervals < 10 ms. These chirps were difficult to count unambiguously and were classified as components of disturbance bursts rather than as separate chirps.

Table 2. Means ± SE of median intervals between stridulatory pulses and durations of randomly selected chirps detected from *L. kitteli* nests that were unstimulated, presented with a prey insect, or exposed to an air puff

Treatment	Interval (ms)[a]	Duration (ms)
Unstimulated	1.64 ± 0.08a (610)	51.1 ± 7.5
Prey larva	1.00 ± 0.10b (1,000)	45.1 ± 8.4
Air puff	1.12 ± 0.07b (893)	57.3 ± 5.2

Median stridulation frequency (in Hertz), calculated as (median interval)$^{-1}$, is listed in parentheses. Means of intervals in a column followed by the same letter are not significantly different under Wilcoxon signed rank test.

[a] For unstimulated ranked with prey, $t_s = 0$, $N = 5$. $P < 0.001$; unstimulated ranked with puff, $t_s = 0$, $N = 5$, $P < 0.001$; and prey ranked with puff, $t_s = 4$, $N = 5$, $P = 0.44$.

noise are shown in Fig. 5. Frequencies <1 kHz had the greatest energy for all treatments and also for the background, as is typically observed in acoustic recordings (Mankin et al. 2011). The frequencies of greatest energy-difference from background were predominantly in two bands between 3.7 and 7.2 kHz (rounded rectangle L in Fig. 5), and 9.5–13 kHz (rounded rectangle H in Fig. 5), and there were no salient differences among treatments.

Discussion

Differences Among Individual Responses to Unstimulated and Prey Larva Treatments. The observations that groups of two to eight *L. kitteli* produce higher rates of chirps (Table 1) and higher rates of stridulatory pulses within chirps (Table 2) during interactions with prey larvae than groups of two to five individuals in unstimulated social interactions are reminiscent of several previous studies. Markl and Hölldobler (1978) reported, for example, that *Novomessor* individuals reacted to presentation of food items, to intruders from other colonies, or to being held with forceps by producing chirps with highly variable durations (a range of 25–200 ms for *Novomes-sor* compared with the 25–95-ms durations observed with *L. kitteli*), and highly variable rates of stridulatory pulses within chirps (200–3,000 pulses per s for *Novomessor* compared with 500–2,500 pulses per s observed with *L. kitteli*). Greater rates of chirps and longer chirp durations were detected when the ants were subjected to the intense stimulation of being held firmly to a substrate. In studies of *Camponotus herculeanus* L. alarm drumming, a similar vibration-producing behavior in carpenter ants, Fuchs (1976) observed that higher intensities of drumming increased the vibrational alarm responses of workers. Barbero et al. (2009a) observed that individual *Myrmica* workers and queens may alter the rhythms, speed, and intensity of stridulations to enhance communication of information. Such observations are consistent with a hypothesis that individual ants of multiple species, including *L. kitteli*, produce stridulatory pulses and chirps at faster rates when strongly versus weakly activated, i.e., their stridulations have potential to communicate information to nestmates about the intensity of stimulation. The finding that *L. kitteli* stridulations in response to brief air puff stimuli have different time courses than those produced during prolonged interactions with nestmates when moving prey larvae into the nest suggests further that stridulatory responses are modulated by the temporal context of their stimuli.

It can be expected that wherever a significant communicatory function for stridulation has been identified, more information is transmissible when stridulation by the transmitting ant is modulated and the receiving ant is capable of interpreting differences in the stridulations detected. Therefore, the capability of ants to produce and interpret modulated stridulatory signals may be subject to positive natural selection in many of the contexts where it has evolved.

A complicating factor in considering the communicative role of stridulatory signals in ants is that, often, stridulation does not seem to elicit a specific behavioral response in nearby coworkers, but instead to
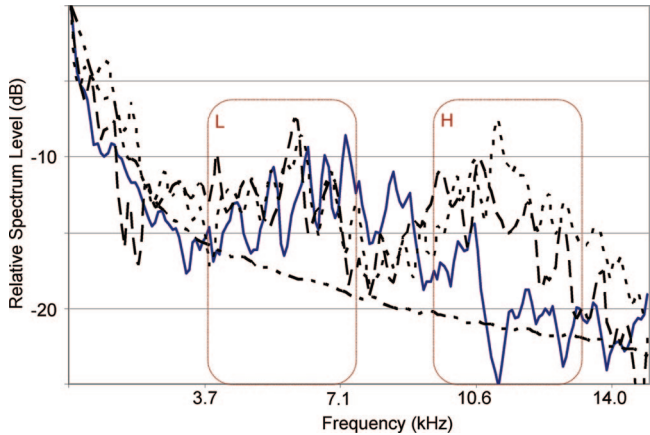

Fig. 5. Spectra of background noise (dash-dot-dot line) and stridulation chirps recorded from unstimulated (solid), prey larva (dashed line), and air puff (dotted line) treatments; rounded rectangles mark secondary peaks between 3.7 and 7.2 kHz (L) and between 9.5 and 13 kHz (H). (Online figure in color.)

modulate their response quickly to other stimuli, including pheromones, food items, or external disturbances (Markl and Hölldobler, 1978). Also, some of the functional roles of stridulation in the behaviors of different species may not involve communication. Rauth and Vinson (2006) found that *Solenopsis invicta* Buren stridulated primarily during excavation activities, although individuals also stridulated when they were constrained. The communicatory contexts of social interactions, food recruitment, and alarm are considerably different from those of excavation behaviors. *Leptogenys* may be a particularly informative genus in this respect because it contains some species with and some without stridulatory organs (Markl 1973). It is of interest from an evolutionary perspective to consider the contexts of stridulatory behaviors in multiple *Leptogenys* species that have stridulatory organs and compare how those contexts have been altered in species that have lost their stridulatory organs.

Chirp and Disturbance Bursts as Potential Indicators of Collective Stridulation Activity. Chirp bursts were not observed in unstimulated treatments and disturbance bursts were not observed in either unstimulated or prey larva treatments (Table 1), so the occurrence of chirp and disturbance bursts in a recording is potentially an indication that groups of ants are producing stridulations simultaneously. Consider, for example, that the inverse of the $1.7\,\mathrm{s}^{-1}$ mean chirp rate in Table 1 corresponds to a mean chirp interval of ≈ 0.6 s. A group of 10 ants producing chirps at an average rate could easily produce a chirp burst with intervals of 0.06 s, and a group of 60 ants could produce a disturbance burst with chirp intervals of 0.01 s. Such results are supportive of the estimates presented in the Results that two to five ants were interacting in the unstimulated treatments, two to eight in the prey larva treatments, and 20–100 in the air puff treatments. It should be noted however that because individual ants can be highly variable in their rates of stridulation, a single ant conceivably could produce chirps at rates that would be acoustically detected as a chirp burst or perhaps even a disturbance burst occasionally.

Potential for Vibrational Signaling of Caste. Evidence from studies of lepidopteran larvae that acoustically mimic ant stridulations (DeVries 1990; Travassos and Pierce 2000; Barbero et al. 2009a,b) suggests that stridulations may be capable of signaling information about the caste and nutritional status of a signaling ant. It is thus of interest to consider features of *L. kitteli* stridulations that may differ between workers and queens. Considering only spectral features, the lower, 3.7–7.2-kHz secondary energy peak of a chirp (see rounded rectangle L in Fig. 5) possibly could provide some information about caste because it does not seem to vary significantly when workers are exposed to different treatment stimuli, but can be expected to vary between queens and workers, due to differences in gaster size. Masters et al. (1983) determined that the lower secondary energy peak typically observed during ant stridulation is caused by pendulum-like vibrations of the gaster, and the upper peak,

the 9–13-kHz band in this species (see rounded rectangle H in Fig. 5), probably is produced by spherical pulsations of the gaster. The queen has a larger gaster and consequently would be expected to have lower frequency secondary energy peaks than her workers, as was found by Barbero et al. (2009a, b).

However, this observation must be placed in context. For example, it is known from studies by Markl (1970) that ant subgenual organs can detect frequencies only up to ≈ 4 kHz. Receptors sensitive to frequencies above seven kHz have never been identified; consequently, such signals are not likely of behavioral relevance to the ants. In addition, because the high-frequency components of vibrations attenuate rapidly with distance in sand and in plants (Virant-Doberlet and Čokl 2004, Cocroft and Rodríguez 2005, Hill 2009); vibrations <1 kHz typically are of greatest behavioral relevance for communication.

Given the strong likelihood that *L. kitteli* workers would not detect or interpret high-frequency spectral differences in the stridulations of queens and workers, a more likely mechanism for signaling information about caste in this species would be potential differences in temporal patterns of stridulation. These kinds of mechanisms have been identified in social wasps, for example, where it has been found that differences in temporal patterns of antennal drumming on the rims of larval nest cells affect subsequent emergence as workers or as reproductives (Suryanarayanan et al. 2011a). However, it remains to be determined whether spectral features, chirp rates, or stridulatory pulse intervals confer any information about caste status in this species.

Vibrational and Pheromonal Communication. Considering the functional importance of pheromonal communication in ant colonies (Vander Meer and Alonso 1998, and references therein), it is of interest to consider whether results in this study provide any perspective on the functions of stridulatory signals in relation to pheromonal signals. An example is alarm pheromone that alerts nestmates rapidly to perturbations or stresses. Such signals are similar in function to disturbance bursts produced after air puffs. Disturbance bursts in *L. kitteli* and many other ants are transient signals, declining rapidly within 10 s. However, alarm pheromones frequently are transient signals also, so it is not certain why one signal would be used concurrently with or in preference to the other. In both cases, the responses of nestmates depend on other stimuli and the behaviors they are performing when the alarm is initiated (Markl and Hölldobler 1978, Vander Meer and Alonso 1998).

One possible explanation for concurrence of pheromonal and vibrational signals is that the signals could reinforce each other as multimodal stimuli. Stridulatory signals are active over shorter distances than pheromones (Markl and Hölldobler 1978), so they may help to focus the responses of nestmates to alarm pheromones. In addition, the vibrations induced in the ant exoskeleton by the stridulatory signals could help volatilize and increase the effectiveness of the alarm

pheromone, as considered previously for tephritid sex pheromones (Mankin et al. 2008a).

Co-opting Vibrational Communication for Pest Control. The large number of different functional roles for which stridulation has been implicated in colony activities may provide some opportunity for incorporating artificially produced stridulations into pest control measures. Two immediate applications are suggested by the roles of stridulation in food-retrieving behavior and in the induction of colony emigration. For some ant species, cooperative efforts of carrying bait into a nest are enhanced when foraging ants that contact the bait detect vibrations produced by other nestmates (Markl and Hölldobler 1978). Low-power piezoelectric buzzers and actuators already are available commercially (Uchino 2008) or can be custom-built (Suryanarayanan et al. 2011b), and small, disposable devices possibly could be developed to vibrate ant baits externally and facilitate their movement into a nest.

Also, because vibrational signals are used by some ant species during emigration to new nesting sites (Maschwitz and Schönegge 1983, Witte and Maschwitz 2002), it may be feasible to use vibrations with particular temporal and spectral patterns to induce emigration from telephone or electronic equipment housings used as nesting sites (Eagleson 1940, Vander Meer et al. 2002) particularly if mechanical vibrations are stressors that affect the levels of biogenic amines (see Jeanne 2009, and references therein). The species- and context-dependent qualities of stridulatory communication would be complicating factors in development of these kinds of control measures. However, many ants in addition to *L kitteli* (Table 2) are known to produce 0.5–1.5-kHz stridulation frequencies, including two *Novomessor* species (Markl and Hölldobler 1978), *Atta sexdens* L. (Masters et al. 1983), four *Myrmica* spp. and *Atta cephalotes* (L.) (DeVries and Cocroft 1993), *Solenopsis richteri* Forel (Hickling and Brown 2000), *S. invicta* (Mankin and Benshemesh 2006), and three other species of *Myrmica* (Barbero et al. 2009a). Consequently, frequencies in this range also may be useful for investigations with species other than *L. kitteli*. Such effects have been observed previously in termites (Inta et al. 2009), where a reduction in feeding occurred after playback of disturbance head-banging recordings.

Acknowledgments

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