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SOUNDS PRODUCED IN PUPAE OF LYCAENIDAE

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Sound production by pupa of the Lycaenidae and Riodinidae is known for over 160 species (Downey and Allyn, 1973) representing a broad spectrum of diverse taxonomic groups within the families, and individuals from every major biogeographical realm. It is postulated that most of the species in these families, variously estimated at between 5,000 and 8,000 are capable of pupal sound production. The noise has been known for over 200 years (Hinton, 1948) but as far as we know only one other attempt has been made to closely analyze the sounds emitted. Hoegh-Gulbert (1972) provided detailed audiospectrographic analyses and laboratory experimentation with six lycaenids from Denmark.

Pupal sounds are produced in the intersegmental regions of the abdomen, particularly the area between segments 5 and 6, but sometimes also from intersegmented clefts 4/5 and 6/7. The dorsal part of these regions may have better developed stridulatory devices than lateral and ventral areas. Details of the structures involved may be found in Downey (1966) and Downey and Allyn (1973). Suffice to say here that sound is usually produced by the movement of a posterior intersegmental component (file) containing numerous teeth, against an anterior intersegmental component (stridulating plate) which contains the grating surface. Since the pupae are round in cross-section, and each posterior abdominal segment is somewhat telescoped into its adjacent anterior segment, any type of motion could conceivably rub opposing sound producing elements. Rapid movement (trembling, vibratory pulsing, telescoping or bellowing) of the two components produces a frictional impact between the teeth and the grating surface with the resultant vibration of the integument and sound.

While the teeth and stridulating plate are ultrastructural components of the integument, the sound resonators may be vibrating a large part of the body of the pupa. Such a system has been identified in adult triatomine bugs (Schofield, 1977) and in ants (Markl, 1968), and it is possible that the entire pupa is acting as an auxiliary sound radiator, producing a wide frequency range containing harmonically unrelated components. What effects silk webbing (girdles, cremastral pads, etc.) attached to the pupae might have in dampening emitted sounds is uncertain, but it is acknowledged that removing the pupa from its natural site, and placing it loosely on glass, plastic, foam, or microphone substrates may alter certain of the characteristics of the sound.

A recording stylus will pick up vibrations on segments adjacent to the intersegmental areas in which the sound structures are located. This indicates the likelihood of induced vibrations elsewhere in the body, which complicates laboratory analysis of component signals.

Sound from some pupae was so attenuated as to be virtually inaudible without a reflecting vial, or directional microphone. With both of the latter devices microphonic artifacts and mechanical problems (standing waves, vibrations, etc.) made suitable analysis of the frequency spectra of the initiating signal meaningless.

Harmonically related components were detected, but all were proved to be associated with reflecting surfaces and not from the insect source.

Methods and Equipment

Two different microphones were used to pick up the pupal sounds: a Sony ECM-50 Electret Condenser Microphone and an Electro-voice C085 Condenser Microphone. For much of the study the ECM-50 was converted to a highly directional unit by fitting paper tubes of varying lengths to the microphone.

Signals were also recorded using an Astatic stylus number 91T applied directly to the pupal integument.

The sound inpulses were fed to a Dukane high fidelity preamplifier and audio amplifier and recorded on an Akai 1722 W tape recorder at 95 mm per second using BASF low noise recording type.

Although most of the observed sounds were recorded, direct observations were also made using a Tektronix 5103N oscilloscope with a D11 single beam storage unit, and simultaneously analyzed using an EMR 1510 real time spectrum analyzer having a frequency range from 25.6 Hz to 25.6 KHz.

Uniform conditions were maintained at all times during collection of data except where noted. Laboratory facilities were maintained at 74° F (23.3°6).

Sex of the pupa was established only on emergence of the adult and subsequently associated with recorded or analyzed data.

Results

At least three forms of sound emission were identified in most of the lycaenid species critically examined. These are designated as primary, secondary and tertiary signals, and are usually distinguishable in particular pupae by distinct differences in amplitude, as well as other criteria: *primary signals* are audible to the human ear, have a duration of from 5ms to 50ms, may be elicited by several stimuli (agitation, touch, static field, sound, etc.), and consist of a varied range of repeated responses (pulses) from one to several dozen over several minutes duration; *secondary signals* are mostly inaudible to the human ear, have a level of amplitude peaking at nearly half that of the primary signal, may be described as a series of staccato, rapidly repeated elements (rather like a short burst of machine gun fire) in pulse trains varying from 12 to 20/sec., and cannot be induced (except in the broadest sense); secondary signals in some species may consist of a "buzz" or "whirr" which so far defies audiographic analyses, but which only occur in those species in the absence of the staccato elements described above; *tertiary signals* consist of elements barely above the amplitude range of "background noise", about half the voltage displacement of the secondary signals and are produced rather continuously with an irregular cadence. They increase in speed with agitation, without, however, affecting amplitude or irregular pattern. Tertiary signals seem to be continuous and not interrupted by primary or secondary emissions.

The problems created by working with the exceedingly low levels of sound and the difficulty of eliminating all traces of reflective and standing wave forms proved to be insurmountable under the experimental conditions available. For this reason we do not believe that the frequency data obtained for each species were reliable. Frequency data were thus omitted from the species accounts below.

Hoegh-Guldberg (1972, pg. 135) discounted "resonance phenomena" in recording vials by finding "reasonable agreement" between "vibration sonagrams" obtained directly from contact with the pupae and "recording sonagrams" recorded with a microphone. However, we were able to observe only random noise output by stylus contact methods, which consisted of frequencies up to 3.5 KHz. This corresponds quite well with microphonic observations with *L. hyllus* and is consistent with data obtained on all other species.

For each species considered below, a reciprocal ratio of sound amplitude for the three types of sounds is given. That is; a 1:2:6 ratio indicates that the secondary signal was twice as loud as the tertiary, and the primary signal was 6 times louder than the tertiary signal for the particular species. These ratios were obtained from compiled data and averaged for each species. Other data on character, duration and periodicity are also given below.

Callophrys henrici (Grote & Robinson)

C. henrici produced all three signal forms (Fig. **1**). The primary signal was readily audible and can be induced by physical agitation or low level sound from 100 Hz to 3000 Hz. No response was obtained to frequencies above 3000 Hz. Strangely the *henrici* pupae did not respond to either 200 Hz or 2000 Hz even though the levels were substantially increased.

Specimens examined in 1975 had very short primary signal duration times, frequently no longer than 6 ms. In 1977 pupae from the same site exhibited much longer signal durations (average 26 ms) (Fig. **2**).

The secondary signal was not observed in 1975 pupae sampled, but was uniformly present in the 1977 specimens (Fig. **1**). Each pulse duration averaged 2 milliseconds and the signal spacing was quite uniform, having 12 impulses per second. This signal was barely audible without amplification in these relatively large pupae.

The tertiary signal (Fig. **3**) was noted in all specimens examined and had signal durations of 2 - 4 milliseconds. No difference was detected between specimens obtained in different years.

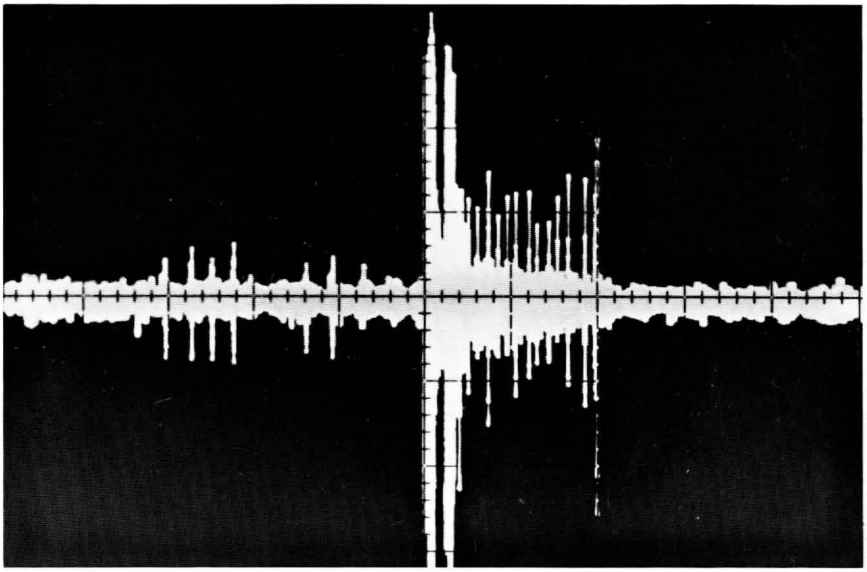

Fig. 1 Oscilloscope trace (5 second total sweep) of *Callophrys henrici* showing the three types of signals characteristic of many lycaenid pupae. The primary signal with the largest amplitude is at the center of the sweep; tertiary pulses are at the left of this and secondary pulses, with medium amplitude are directly to the right, and were initiated at the same time as the primary signal.

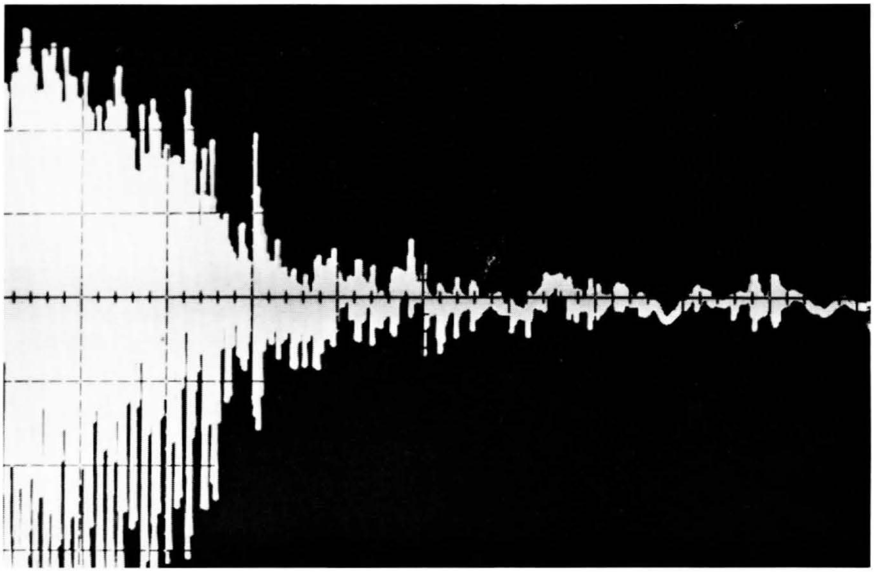

Fig. 2 Expanded primary pulse of *C. henrici* with a duration of 32 ms; average is 26 ms. 100ms total sweep.

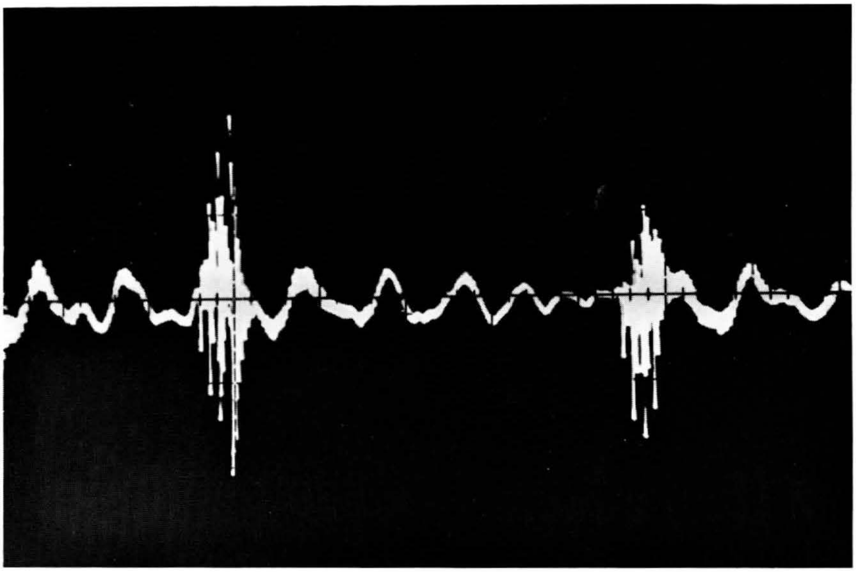

Fig. 3 Expanded tertiary pulse of *C. henrici;* 100 ms total sweep.

The amplitude ratio for *C. henrici* is 1:3:6.

Chlorostrymon simaethis (Drury)

All three forms of signals occurred in *C. simaethis*. The primary form was readily audible and was of rather long average duration (38.0 milliseconds) (Fig. **5**). The impulses were regularly spaced (Fig. **4**). It was not possible to obtain responses by means other than physical agitation. The duration of signal decreased with age of pupa (Table **1**).

The secondary signal was somewhat more variable than other species having 13-14 pulses per second, with an average duration of 8 milliseconds per pulse.

The tertiary signal was quite weak and had a pulse duration of an average

Pupation Day	Duration Primary Pulses/ms	No. Pulses Observed
1	43.2	147
2	41.4	55
3	35.2	89
4	34.2	70
5	35.2	29
6	29.8	22
7	29.0	10
8	31.7	9
9	35.0	8
10	emerged	----

Table 1. Pattern of duration of primary signal with age of pupae in *C. simaethis*. Difficulty in obtaining responses accounts for the decrease in numbers of observations during the test period.

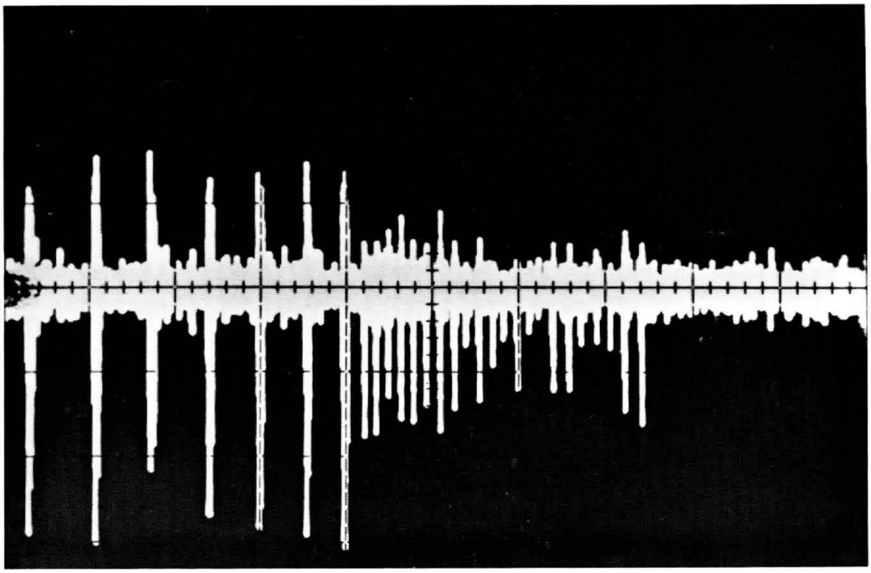

Fig. 4 Oscilloscope trace (5 second total sweep) of *Chlorostrymon simaethis*. Only primary and secondary signals are apparent.

of 4 milliseconds. Because of the very low energy level of this signal, we could only approximate its voltage displacement, thus giving an amplitude signal ratio of 1:2:4.

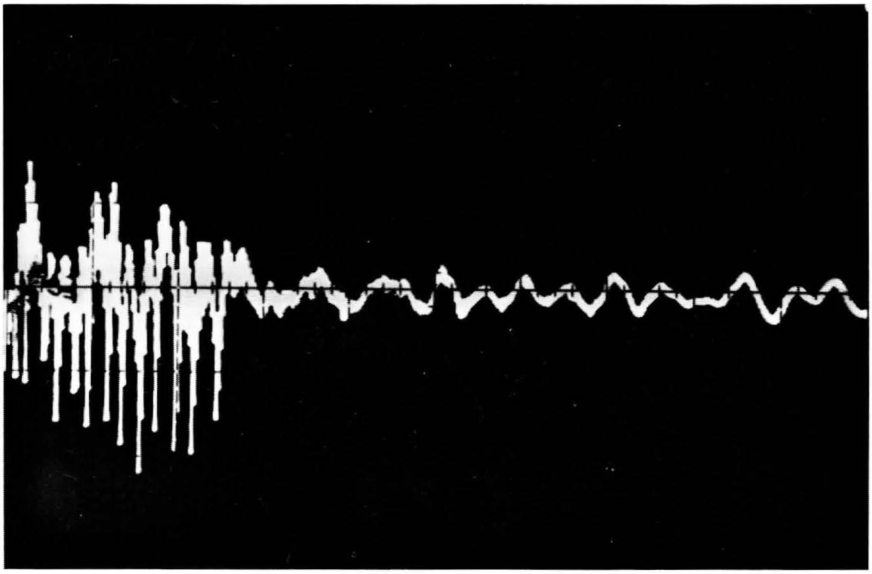

Fig. 5 Expanded primary pulse of *Chlorostrymon simaethis* with a duration of 27 ms; average duration is 38 ms in this species. 100 ms total sweep.

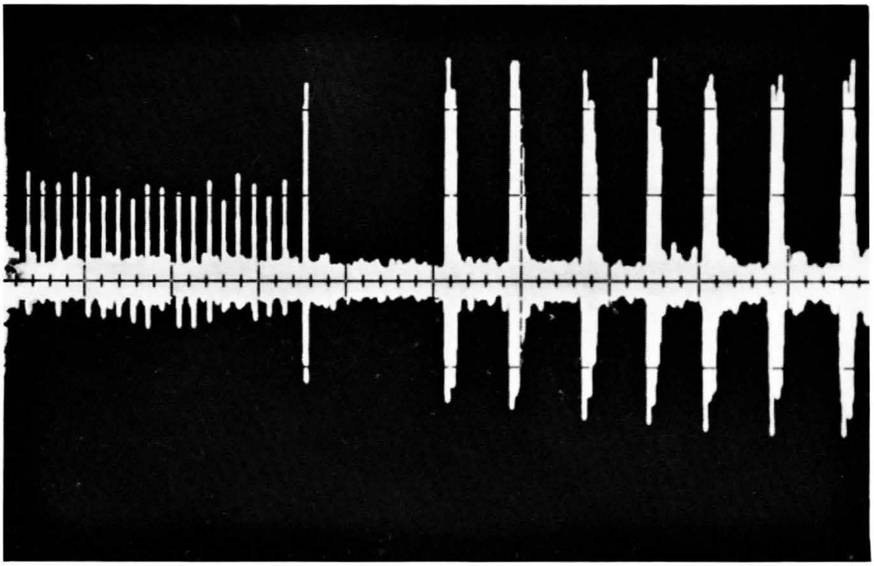

Fig. 6 Oscilloscope trace (5 second total sweep) of *Strymon melinus*. Primary and secondary pulses are readily noted.

Strymon melinus Hübner

The sound producing activity of these pupae was extremely good and permitted the collection of superior data. The primary signal had an average duration of 42.2 milliseconds at room temperature (Fig. **7**). When the temperature was raised to 95° F (35°c) the duration was reduced to an average of 21.1 milliseconds. Upon return to room temperature the signal duration recovered to an average of 40.8 milliseconds. The amplitude of the male specimen signal significantly exceeded that of the female. The signal duration and amplitude of both sexes declined with pupal age. The pupae responded to sound signals of 1 KHz, static field change and physical agitation.

The secondary pulses (Fig. **6**) occurred at a rate of 14 per second with a single pulse duration of 4.7 milliseconds. While the amplitude of the male signal exceeded that of the female, no sexual difference in pulse rate was noted.

The tertiary signal, though weak, had an average duration of 4.8 milliseconds and was irregular.

The amplitude ratio of the signals was 1:2:4.

Lycaena hyllus (Cramer)

Five pupae examined exhibited only primary (Fig. **8**) and tertiary signals. A sixth specimen had both of these signals but was unique in producing a distinct secondary signal having a whizzing sound not characterized by the more common staccato impulse. The latter sound could not be analyzed audiographically.

Primary signal duration of the females was slightly longer (33.5 ms) than the male (28 ms). At 95° F (35°c) the female signal duration decreased to an average of 24.7 ms. It is presumed that the same decrease might be observed in the male.

Primary signal amplitude appeared to decline with pupal age in both sexes.

The tertiary signal was strong and of almost the same amplitude as the primary signals of species having smaller pupae (*E. comyntas, L. cassius*). The duration of

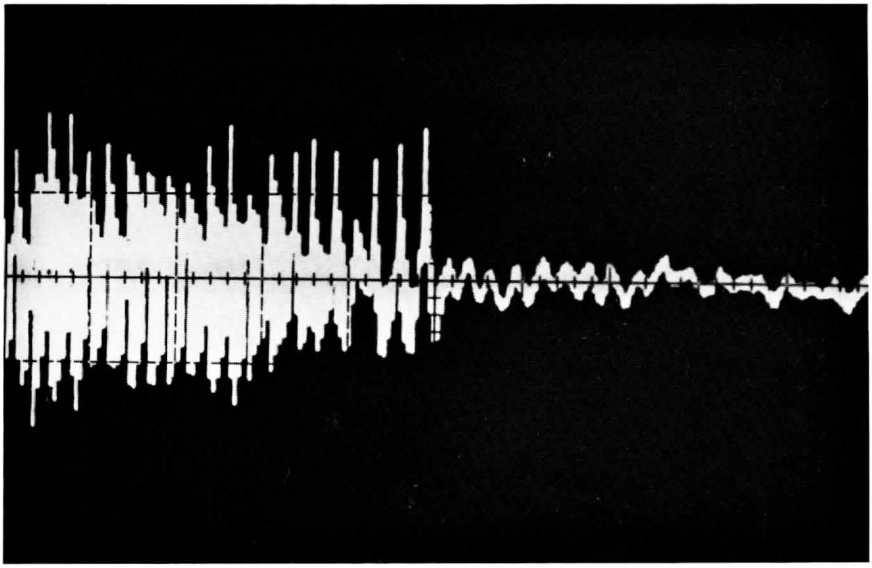

Fig. 7 Expanded primary pulse of *Strymon melinus* with a duration of 50 ms. 100 ms total sweep.

each pulse of this signal was 15 ms in the male and 28.3 ms in the female. As was observed in the primary signal, duration of the tertiary signal of the female was reduced to 21 ms when the temperature was increased to 95° F (35°c).

The ratio of amplitudes was found to be 1:6.

L. hyllus pupae did not respond to sound stimuli, but were extremely sensitive to static field variation and to physical agitation. Variation in the magnetic field seemed to have no effect on the sound producing behavior. The rather loud and easily induced noises of *L. hyllus* enabled us to work many hours with individual pupa and demonstrate repeatedly that the primary and tertiary forms of sound were essentially random noise with the predominate range of frequencies between 800 Hz and 4600 Hz. Small peaks were evident but not significant. We suspect that all the species examined to date produce random noise.

Leptotes cassius theonus (Lucas)

L. cassius theonus produced all three distinct types of sound (Fig. **9**). Primarily because of the small size of the pupae these sounds were of exceedingly low level and the primary form was only barely audible without high amplification. All data were obtained from substantial numbers of local populations over a three year period. A population from St. Augustine, Florida was sampled, but no significant differences in sound production were observed.

The duration of impulse of the primary sound was an average of 10.4 ms (Fig. **10**) in males and 12.6 ms in females. In both sexes the duration of pulse decreased with pupal age except for two specimens, which unaccountably increased dramatically. This decrease was also noted in other species (see Table **1**). When the temperature of the environment was increased to 95° F (35°c), the signal duration was decreased to an average 9.3 ms.

The secondary signal consists of staccato pulses averaging 1.5 ms duration and occurring at the rate of 20.5 per second. At 95° (35°c) the pulse rate increased to 36 per second.

The tertiary sounds were only barely detectable and were at first thought to

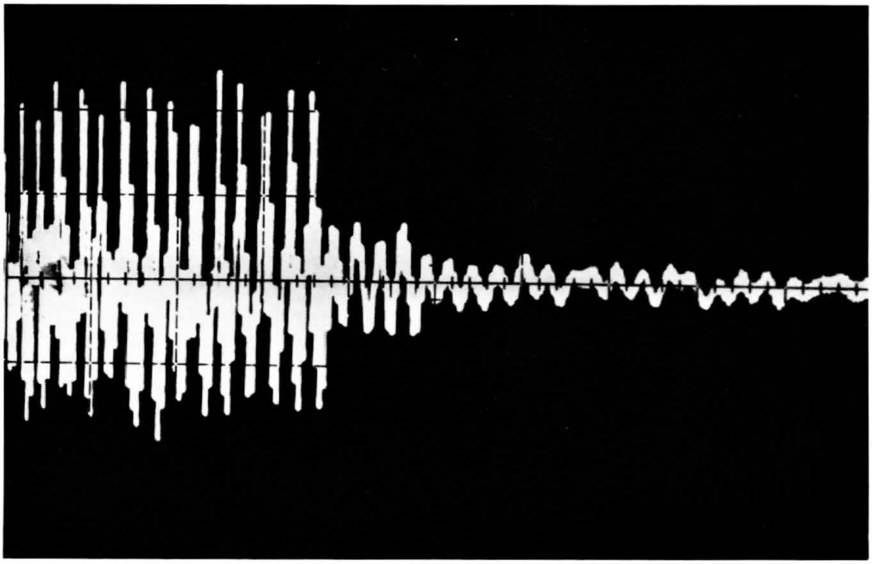

Fig. 8 Expanded primary pulse of *Lycaena hyllus* (=*L. thoe*) with a duration of 36 ms; the males averaged 28ms duration. 100 ms total sweep.

be line noise from the power source. Subsequent analysis proved them to be a constant part of the sound repertoire of the pupae. Signal duration was not readily measurable, but is believed to be of the order of 1 ms.

The sound level ratio of the three signals is approximately 1:2:6.

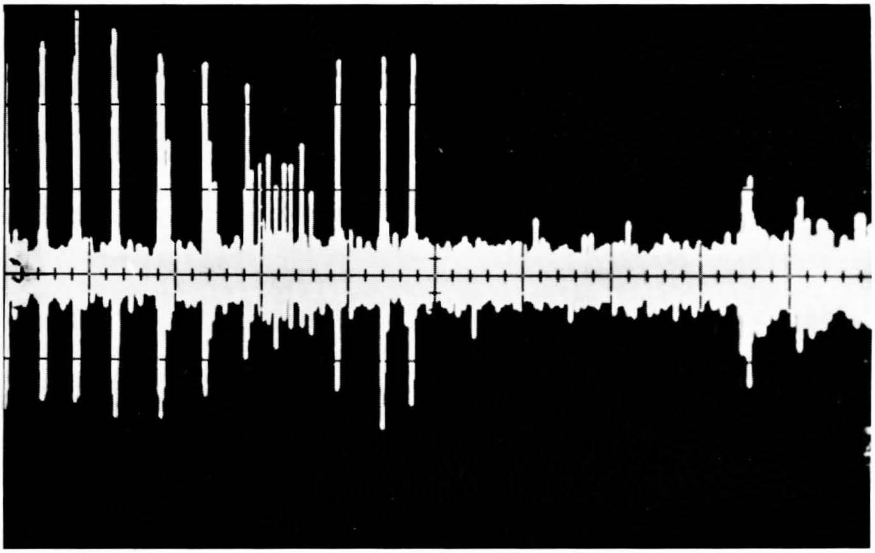

Fig. 9 Primary and secondary pulses of *Leptotes cassius* (5 second total sweep). The secondary pulse starts at the same time as a primary signal.

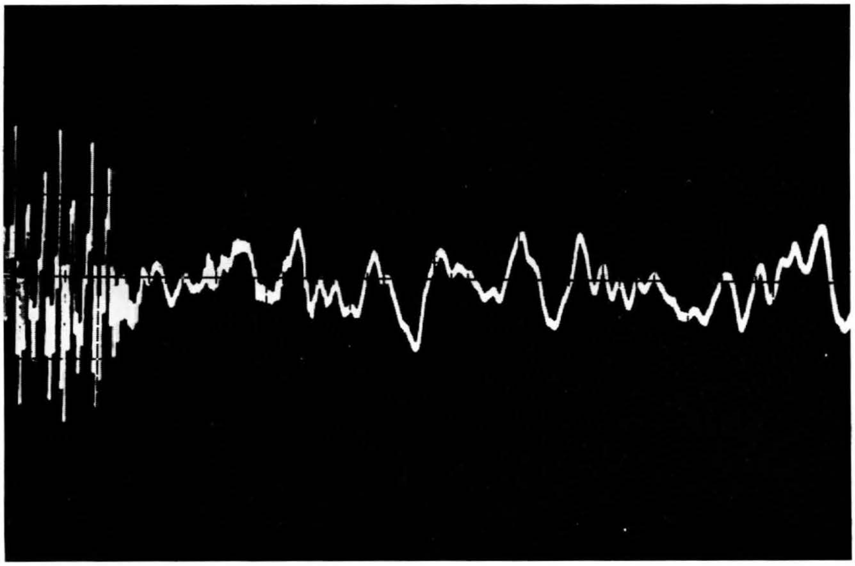

Fig. 10 Expanded primary pulse of *L. cassius* with a duration of 10.4, which is also the average for this species. 100 ms total sweep.

None of the pupae responded to other than mechanical stimuli.

Hemiargus thomasi (Clench)

The duration of the primary signal was extremely variable; average ranged from 3.7 milliseconds to 16.8 milliseconds (Fig. **11**). There were frequent double pulses which were very difficult to separate analytically and which could indicate a reason for the observed high variability of signal duration.

The secondary signal was very faint and did not have the staccato character most often encountered in other species. It had a sound more like a faint buzzing lasting at most for 2 seconds. Accurate date concerning its form were not obtainable.

The tertiary signal was exceedingly faint although its signal duration was measurable at an average of 5 milliseconds.

Amplitude ratio could not be determined.

Everes comyntas (Godart)

The primary signal has a duration averaging 21.7 ms. (Fig. **12**).

Probably due to the small size of the pupae, the amplitude of the other sounds was very low. For example, the secondary signal was audible only at maximum amplification, and the background noise precluded any accurate analysis. However, it was heard as a whirring or whizzing sound which presented difficulty in analysis in other species where encountered.

Similarly the tertiary signal was observed as an almost imperceptible clicking unsuitable for analysis.

DISCUSSION

It has been reported (Hoegh-Guldberg, 1972) that pupal sounds are composed of series of frequencies from 400 Hz to 5500 Hz. Detailed examination of recordings and

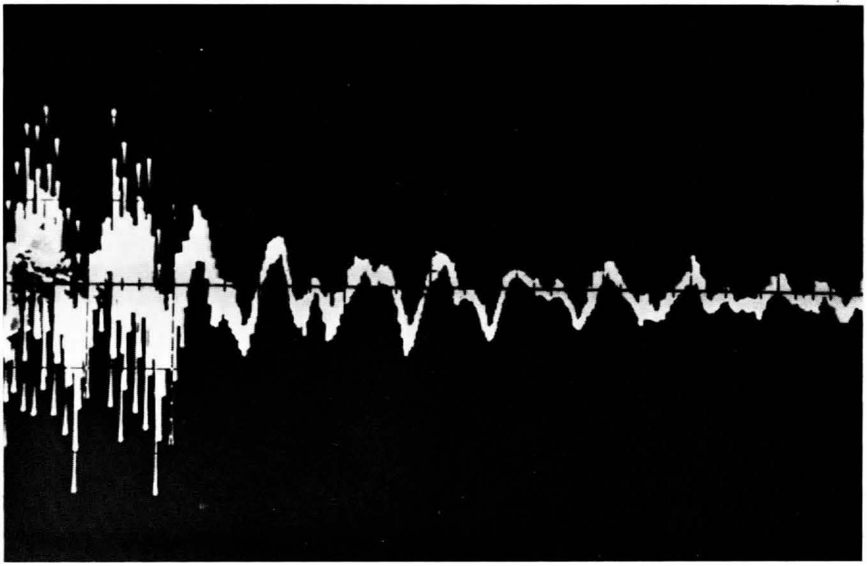

Fig. 11 Expanded primary pulse of *Hemiargus thomasi* Clench. Note "double-pulse" which caused some difficulty in establishing duration of signal. 100 ms total sweep.

direct analyses of the various pupal signals led us at first to believe that specific frequency patterns were indeed present. In order to be certain that our laboratory conditions were adequate for such analyses, we experimentally varied these conditions, and were convinced that the frequency peaks observed were, in truth, artifacts.

Experimenting with the closed microphone-pupa system demonstrated very clearly how easily sound artifacts may be created. By varying the column length the apparent frequency output could be drastically changed. Unfortunately, we were unable to devise a method which would permit the recording of the secondary or tertiary signals without resorting to the use of a closed system.* We can therefore only guess that there probably are no definite frequency peaks in the secondary or tertiary signals.

When specimens were obtained whose primary signal was of sufficient amplitude to permit open observation without any potentially reflective surfaces, except the microphone and the pupa itself, the responses were random noise without significant frequency characteristics.

Using stylus sensing apparatus in direct contact with the stridulating segments, it was discovered that the sounds produced were also random noise. *Strymon melinus* appeared to have some broad differentiation in amplitude between 2 KHz and 3.5 KHz, but no clear peaks were discernable.

An SEM examination of the stridulating structure (Downey and Allyn, 1973) tends to support a view that the stridulating surface might well be incapable of producing other than random noise.

Recordings were made of pupal sounds immediately prior to and during emergence. We were unable to find any significant differences in signal form or frequency prior to emergence. The splitting of the pupal integument and the leg movements of the emerging imago were visually related to certain different sounds created during emergence.

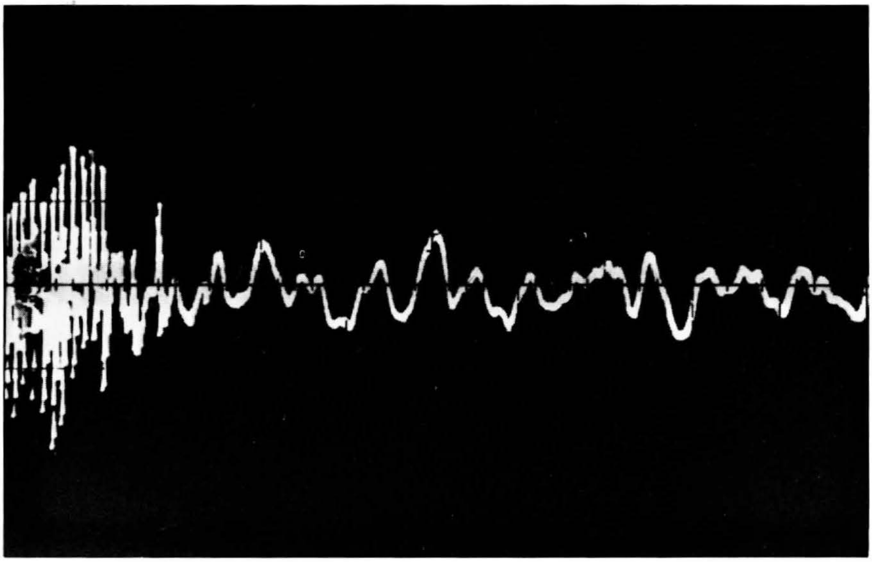

Fig. 12 Expanded primary signal of *Everes comyntas*. This sample has a duration of 12.6 ms; average is 21.7 ms for this species. 100 ms total sweep.

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*While seemingly obvious and elementary, future workers are cautioned regarding these mechanical problems, which may continually distort the sounds produced by the individual pupa.

The tertiary signals in all species observed were emitted continuously and had an irregular cadence with no discernable pattern. On agitation neither the amplitude or lack of pattern was changed although the cadence was accelerated.

The signal continues without interruption during the emission of primary or secondary signals suggesting a different production site. It has been suggested to us that these faint irregular sounds are not unlike the sounds of involuntary muscle contractions in vertebrates.

SEM examination of the stridulating surfaces of the pupa have revealed several potential sites for the primary activity other than the 5/6 intersegmental surfaces though none appear as well developed. Downey has previously reported visual correlation between the 5/6 segmental movement and sound production. It is possible that the tertiary sound source could be one or more of the other observed sites.

The staccato or buzzing signals which have been designated as secondary signals (primarily because of their amplitude) usually occur following a primary pulse but may be initiated independently by the pupae. We have not observed this pulse train being ended by emission of a primary pulse, but not infrequently it is ended by a pulse of higher amplitude, which, because of its short duration, can be considered a part of the secondary pulse train. We have not observed an interruption of the secondary pulse train by a primary signal suggesting that the production site of both primary and secondary signals may be the same. Tertiary signals occur throughout the emission of secondary signals.

Mr. N. W. Elfferich of Copenhagen, kindly supplied us with two tapes containing the sounds recorded by him of the following Palearctic species:

Palaeochrysophanus hippothoe (Linné)
Lycaeides idas (Linné)
Polyommatus icarus (Rottemburg)
Maculinea nausithous (Bergsträsser)
Maculinea alcon (Schiffermüller)
Lycaena phlaeas (Linné)
Lycaena dispar (Haworth)
Lysandra coridon (Poda)

From these tapes we were only able to discern primary signals. Attempts were made to critically analyze these signals, but strong evidence of artifact creation prevented reliable inferences. The primary signals seemed to be of the same nature and duration as those of the Nearctic species examined and reported herein.

Of particular interest is the fact that the two species of the genus *Maculinea* which have internidal pupae exhibited essentially the same primary signal as non-nest dwelling species.

We further postulate that tertiary and possibly secondary signals occur in these Palearctic forms and the sounds will prove to be random noise without significant frequency peak.

CONCLUSIONS

Detailed spectral analyses of sounds produced by pupae of seven unrelated species of the family **Lycaenidae** indicate the following.

(1) While the sound structures are located in the intersegmental area (4/5, 5/6, 6/7) of the abdomen, vibration of the pupal integument causes a larger area of the pupa to act as an auxiliary sound radiator capable of producing a wide frequency range containing harmonically unrelated components. This range is from 400 Hz to 5 KHz.

(2) Three forms of sound were noted in most species examined which can be distinguished by differences in amplitude and other criteria: *primary signals* are

audible and are characterized by a rasping chirp of several milliseconds duration, and are emitted irregularly on stimulation of the pupa by either physical or auditory means; *secondary signals* are mostly inaudible without amplification and are characterized by a series of staccato clicks of extremely short duration, but very regularly spaced (machine-gun like); in some species this form of signal becomes continuous and may best be described as a whizzing noise (*L. hyllus, H. thomasi, E. comyntas*); *tertiary signals*, like the secondary ones, are inaudible in all but the largest pupae (*L. hyllus*) and are highly irregular continuous clicking sounds occurring even during the production of the primary and secondary emissions; these sounds are of very low amplitude near the range of "back-ground" noise.

(3) Sound production varied with environmental temperature and pupae age; primary signal duration usually decreased with an increase in temperature, and with the period of time spent in the pupal stadium.

(4) We could not detect differences in sounds produced by several local and one distant population (of *Leptotes cassius*) but an "annual" difference in primary pulses for one population (of *Callophrys henrici*) was noted. The latter involved pulse duration, rather than amplitude, which is less easily explained by such things as pupal size based on nourishment differences, etc.

(5) Differences in sound signals between male and female pupae were noted in some species (*i.e., S. melinus*). However, sexual differences were slight and were judged to be insignificant.

(6) The discovery of the random nature of the noise produced by *Lycaenid* pupae may weaken those explanations of function based on communication signals with ants (Downey, 1966).* We are more inclined toward a predator deterrent (or protective) role for the sound.

ACKNOWLEDGMENTS

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Finally, special thanks to our colleague Dr. Lee D. Miller for suggestions and criticism of the manuscript.

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*One might assume that selective process based on an auditory receipt of pupal signals by ants might favor specific wave lengths. In contrast, where the function is assumed to be mainly as a predatory deterrent where several organisms are involved, random noise with a wide frequency range such as has been shown to be produced, might selectively be more effective than sounds with a narrow level of frequency.

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