Anim. Behav., 1974, 22, 741–744

RHYTHMS IN ACOUSTICAL COMMUNICATION BY THE ORIENTAL HORNET, *VESPA ORIENTALIS*

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Abstract. By analysis of the acoustical spectrum within the nest of the oriental hornet, three distinct and characteristic categories of sounds have been recognized: (a) Hunger signals produced by the hungry larvae through the scraping of their mandibles against the comb cell walls; (b) sounds which the workers, arranged in a 'resting circle' around the queen, produce by tapping their abdomens on the surfaces of the cells. These sounds are temporarily designated as 'the taps of workers facing the queen'; and (c) additional worker sounds, also produced as in (b) but of a different rhythm, which have been designated in earlier publications as the 'awakening taps of workers' (Ishay & Schwartz 1965; Schaudeinischley & Ishay 1968; Ishay & Landau 1972; Ishay & Schwartz 1973). The particular 'beat' (spcificity) of each of the three sound groups has been investigated in an attempt to understand the significance of rhythms as a means of communication among hornets.

The oriental hornet is prevalent in countries of the Mediterranean basin. In the spring, it forms annual colonies which by the end of summer comprise up to several thousand individuals, adult hornets as well as brood. The nest is mostly constructed in the ground and contains several combs which house the brood. Although the nest is ordinarily unilluminated, it is possible for purposes of study and measurement to transfer small colonies to illuminated artificial vesparia without interfering with the regular development or activities of the colony (Ishay, Bytinsky-Salz & Schulov 1967).

Methods

Hornet colonies comprising a queen, twenty to thirty workers and a comb with brood were transferred during the summer to an acoustic chamber built particularly for the purpose of picking up hornet sounds. This chamber isolated external noises from the noises produced within, thus enabling the 'clear' reception and recording of hornet sounds (Schaudinischky & Ishay 1968). The hornet sounds, all solid-borne, were picked up by the use of highly sensitive B & K vibration pick-up accelerometers which have a linear frequency range of 5 to 25 000 Hz. Such accelerometers were fastened on the back of the comb within the nest, the latter suspended elastically from the ceiling of the artificial vesparium contained within the acoustic chamber. Recording of the sounds was made with the use of a Revox G-36 double-track tape recorder which was connected to the accelerometer. Graphic representation of the sounds was by means of Grass polygraph. Playback into the nest of the recorded signal was through a home-made vibration transmitter (Schaudinischky & Ishay 1968).

Results

The Analysis of Recorded Series of Taps

Taps of workers facing the queen. These taps were recorded at sixteen different times from various workers. For the purposes of analysis, we selected three of these recordings, each running for approximately 3 min and yielding series of about 600 taps. Histograms of the time intervals between taps for these series are presented in Fig. 1 (bottom). The median interval between taps for these series are 0·17, 0·17 and 0·23 s. For two of these curves, 90 per cent of the observations fell between 0·05 and 0·83 s, whereas 50 per cent of the intervals lie between 0·11 and 0·29 s. These values, which are derived from the histogram, emphasize the asymmetry of the distribution and the concentration of the mass of the observations in the neighbourhood of the median.

As the tapping behaviour appears rhythmic, three brief (10 s) series of taps were analysed by power spectrum analysis. This is a method of resolving the variances of the series into components, each of which is the relative amount of the variance explained by fitting to the data sine and cosine functions within a specified band of frequencies. In order to perform this analysis, the relative intensity of the tap was measured from the polygraph readings every $\frac{1}{16}$ s. This data was then analysed by a computer program, BMDO2T (Dixon 1973), to evaluate the power spectrum of the series. A graph of the logarithm of the power spectral estimates for one of these series is shown in Fig. 2 (bottom). Two of the three spectra analysed had sharp peaks at a frequency of 0·060 cycles per 10 ms; that is, a rhythmic frequency concentrated at six taps per second. This agrees very well with the median interval between taps of 0·17 s. The third peak was wider and ended at 0·06 cycles per 10 ms. All three peaks are highly significant, $P<2\%$) (Blackman & Tukey 1958).

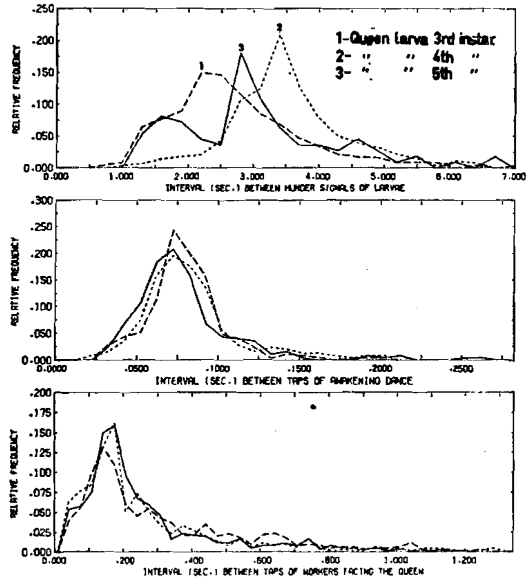

Fig. 1. Relative frequency curves of: top: hunger signals of larvae (three queen larvae of different instars); centre: awakening taps of workers; bottom: taps of workers facing the queen.

Awakening taps of workers. Recordings were made at three times, each from a different worker. Each was of 20-s duration and contained approximately 300 taps. Histograms of the intervals between taps appear in Fig. 1 (centre). The median intervals are all about 0·74 s. Ninety per cent of the observations lie between 0·038 and 0·15 s, whereas 50 per cent fall in the intervals between 0·056 and 0·084 s.

Power spectrum analysis of three 15-s series were performed. (The relative intensity of the polygraph recording was sampled at each 10 ms.) A graph of the logarithm of the power spectral estimates of one of these series is shown in Fig. 2 (centre). The peak of the spectrum appears at 0·012 cycles per ms, that is, a frequency of twelve

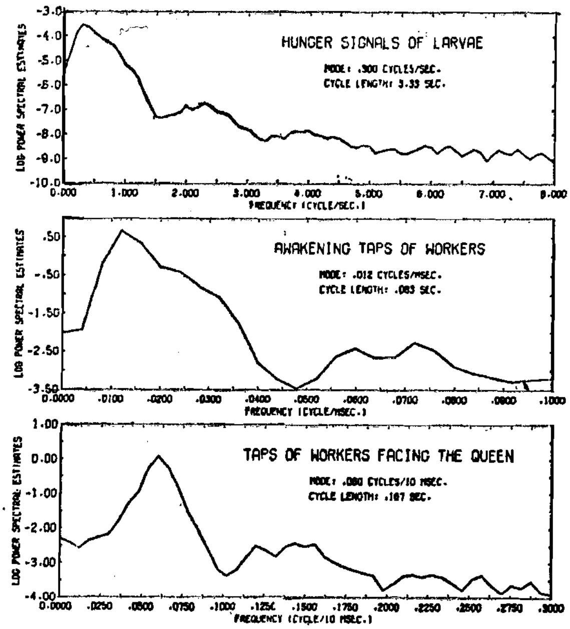

Fig. 2. Rhythm analysis as based on power spectrogram of: top: hunger signals of larvae; centre: awakening taps of workers; bottom: taps of workers facing the queen.

taps per second. Again the peaks were highly significant.

In the awakening dance the taps appear to form clusters, 'bursts', separated by periods of rest. The length of bursts were measured and found to last 1·25 to 2·50 s in duration with a mean of 1·81 s.

Hunger signals of the larvae. The sounds produced by three queen larvae of the 3rd, 4th and 5th instar, respectively, were recorded over a period of 3 hr each. Each series contains about 250 intervals between bodily contractions. Histograms of the frequencies of the intervals are presented in Fig. 1 (top). The medians of the three series are at 2·5, 3·5 and 2·8 s respectively. The distribution of the intervals differ from larva to larva. There is a suggestion from the histograms that a second peak, smaller than the mode, appears at about half the median.

To detect the rhythmic movement of the larvae, six worker larvae (of the 5th instar) were photographed at 16 frames per second. The position of the larvae in each frame was recorded (Ishay & Landau 1972). The power spectrum of a larvae is shown in Fig. 2 (top). The peak of the spectrum is at 0·30 cycles per s; that is, the interval between contractions is about 3·33 s.

Several larvae were starved for a few days and then offered food. For 1 hr per day the noise made by each larva was recorded. Histograms of the intervals between hunger signals produced by one of the larva are given in Fig. 3. The median intervals between contractions were

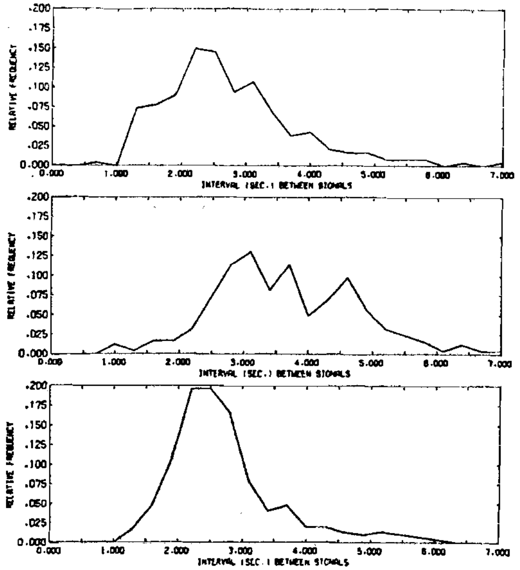

Fig. 3. The effect of starvation on the relative frequency of larval hunger signal. top: after 5 days of starvation; centre: after 7 days of starvation; bottom: after 1 days of feeding following 7 days of starvation.

2·60 (day 5), 3·64 (day 7) and 2·55 (day 8). From the histograms we see that the distribution of the intervals differ from day to day.

Discussion. The three series of taps of workers facing the queen are similar to each other both with respect to the distribution of intervals between the taps and with respect to their power spectra. The awakening taps of workers also are similar one to the other. However, the two types of tapping differs in their frequencies (six versus twelve taps per second). Therefore these results suggest that the pattern of tapping recorded is typical of the behaviour and varies from behaviour to behaviour. It seems reasonable to assume that each pattern represents a form of communication whose content differs from behaviour to behaviour.

The amplitude of the tapping was not studied due to the difficulty of separating it from artifacts. It is quite possible that, if similarly analysed, patterns would also be found in the amplitude.

The Effect on Hornets of Vibrations Simulating Hornet Sounds

Taps of workers facing the queen. When vibrations are sounded which are identical in rhythm and intensity to the taps of workers facing the queen, these vibrations produce several effects: (a) The queen starts moving over the surfaces of the combs or between the combs, apparently in search of vacant cells for oviposition; (b) the workers which had been arranged in a 'testing circle' around the queen go back to nursing or other duties which they are as usually engaged in when in the colony; (c) hunger signals of the larvae cease immediately after the first few vibrations and are not resumed even if the vibrations are continued without interruption for as long as 30 min. To emphasize the significance of this latter finding, we point out that towards the end of summer, the hornet nest contains combs with approximately 2000 to 2500 brood-filled cells. The majority of cells are 'occupied' by larvae of the 4th to 5th instars, which ordinarily produce hunger signals during most hours of the day. Nonetheless, the moment the mentioned vibrations are played at the appropriate rhythm, all larval movement ceases and so also do their hunger signals.

This phenomenon is apparently not dependent whatsoever and will occur inside as well as outside the nest and in darkness as well as in light.

Awakening taps of workers. Simulation of these sounds into the next as vibrations causes a general intensification of activities within the nest. During the hours of nest activity, the effect of the vibration is less pronounced, but even then, more workers are seen to attend the larvae and more larvae produce hunger signals. At night, however, the change is more dramatic in that simulation of the sounds awakens the entire colony. Almost all the larvae commence their hunger signals (which ordinarily are never produced at night), and the workers attempt foraging flights to the field or commence milking the larvae.

Larval hunger signals (Fig. 3). The daytime transmission of vibrations at the rhythm of larval hunger signals into a nest with a normal population, does not produce any detectable changes in larval activity. The workers, however, are seen to pay frequent visits to the vicinity of the vibrator. When the vibrations are played into the nest during the night, the larvae 'reciprocate' with their own signals, and the entire colony awakens. When the vibrations were sounded

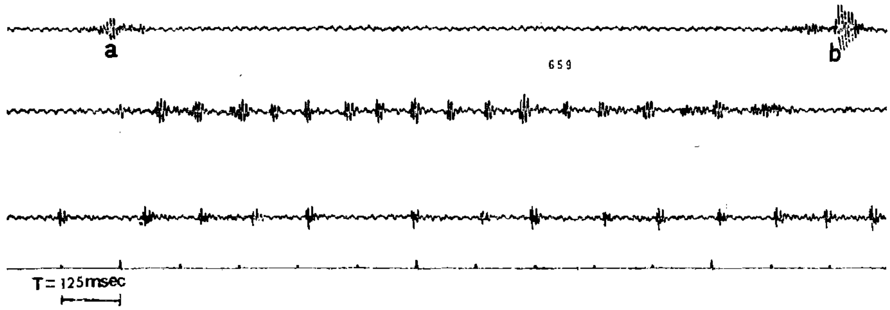

Fig. 4. 'Superposition' of recorded segments of all the afore-described rhythmical phenomena. Top: two larval hunger signals (a and b); centre: the awakening dance of a worker; bottom: the taps of a worker facing the queen.

into a nest containing a brood-comb from which all larvae had been removed and one of the cells was made to house the vibrator, worker hornets were seen to pay very frequent visits to the latter cell, bringing it a 'food offering' of droplets of sugar solution and meat morsels, which were attached to the vibrator rod, as if it were a larva.

Graphic superposition of the three phenomena (Fig. 4). In Fig. 4, we superimpose typical curve segments from each of the three discussed phenomena. The two 'spindles' in the upper portion of the figure were produced by two different larvae. The interval between two signals of the same larva is ordinarily about 3·3 s. However, within this interval, the signals of the larvae may intermittently be superimposed. Regardless of the number of larvae within the comb, the interval between two consecutive signals was almost invariably 2·21/1 s, 3·3/2 s or 3·3/3 s. In the presented drawing, the interval is closest to 3·3/2 s.

As represented in Fig. 4, the length of a 'burst' in the awakening dance does not usually exceed the length of the interval between two consecutive hunger signals, even in cases where the hunger signals are produced by two different larvae. We believe this finding has the following significance: the awakening workers produce a tap between two consecutive larval hunger signals and then pause to allow the larvae to produce their own signals. Possibly, also, the awakening workers at the start of the morning activities, initiate the 'musical rhythm' for the larvae, which then continue sounding their signals throughout the day.

The taps of workers facing the queen, to the extent that we were able to ascertain, are not arranged in 'bursts' but rather occur in an almost monotonous rhythm which tends to stop all other acoustic-vibrational activity in the nest, wherein may lie its communicative significance. In a previous paper (Ishay & Schwartz 1973), we raised the possibility that these taps encourage the queen to continue ovipositing and also supply information, via the distribution of the reflected sonic waves, as to which cells are vacant for oviposition.

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(*Received* 8 *October* 1973; *revised* 12 *February* 1974; *MS. number:* 1258)