

## ULTRASONIC CLICKS PRODUCED BY THE PEACOCK BUTTERFLY: A POSSIBLE BAT-REPELLENT MECHANISM

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### SUMMARY

Torpid peacock butterflies (*Inachis io*) produce intense ultrasonic clicks that startle captive vespertilionid bats (*Plecotus auritus* and *Pipistrellus pipistrellus*). The clicks occur as the wings are opened and are generated by a stiff portion of wing membrane between the costal and subcostal veins near the base of the forewing. The power spectrum of a click matches the most sensitive area of a bat's audiogram. Clicks may serve as acoustic equivalents of the attack-retarding eyespot display in the same species.

### INTRODUCTION

During an attempt to provide captive bats with a varied diet, we observed that the eyespot display of torpid peacock butterflies (*Inachis io* L. = *Nymphalis io* = *Vanessa io*) startled long-eared and pipistrelle bats. During an eyespot display the wings are opened in a characteristic manner, revealing four eyespots on the dorsal surface of the wings (Blest, 1957). The bats' reactions, however, appeared to be related to an acoustic component rather than to the visual component of the display. Since hibernating peacock butterflies are preyed upon by the long-eared bat in nature (Roer, 1969), the observed behaviour might reflect a naturally occurring interaction. This article deals with the acoustic properties of display-coupled clicks produced by peacock butterflies, the mode of click generation, and effects of clicks on bat behaviour.

### MATERIAL AND METHODS

We collected butterflies in Danish hibernating localities from October to December 1974, and maintained them at 5 to 12 °C in the laboratory. About 25 butterflies were used for sound recordings. The insects were put in a small, sound-transparent cage, which in an anechoic room was placed in the centre of an array of four microphones, arranged as corners of a regular tetrahedron. The signals from the microphones (Brüel & Kjaer 4138  $\frac{1}{8}$  in (3.2 mm) condenser microphones) were recorded on a 4-track instrumentation recorder. The overall response of the recording and analysing apparatus was linear within 3 dB in the 1-100 kHz range, as established with a B & K 4142 actuator unit. No corrections were made for microphone free-field response. Absolute sensitivity was referred to a B & K 4230 sound-level calibrator. Peak-to-peak

sound pressure levels are given in dB SPL (re.  $2 \times 10^{-5}$  N/m<sup>2</sup>), measured at a distance of 8–10 cm. The relation between the polarity of actual sound pressure and the recorded electrical equivalent was established by driving the microphone with the actuator from a low-frequency square-wave source. Analyses of waveform and spectra were made from 8-bit digitized versions of the signals, obtained from slow-speed playbacks of the recordings at an effective rate of 640000 samples/s. Power spectrum measurements were made according to the method of Trampe-Broch & Olesen (1970). To determine the location of the sound source, the differences in arrival times of the sounds were read from a storage oscilloscope and processed to render  $x$ ,  $y$  and  $z$  co-ordinates. For clicks originating in the centre of the array, the sensitivity was better than 1 mm. The accuracy depends both on trivial error sources (that are related to equipment and in principle can be calibrated), and on non-trivial error sources, caused by the interaction of body and wing structure with sound propagation and anisotropic radiation. These latter error sources are not quantifiable. Sounds produced by the insects triggered an electronic flash allowing us to record the insects' positions and postures on photographic film or videotape.

In our behavioural studies we used three vesperilionid bats, two pipistrelle (*Pipistrellus pipistrellus* Schreber) and one long-eared species (*Plecotus auritus* L.). The bats were kept in small cages and fed mainly on meal-worms. The bats were not in torpor during experimentation. About 15 butterflies were used in many presentations to the bats.

#### RESULTS

The insects displayed when stimulated visually by quick hand movements towards the head or by lightly touching the legs, thorax, head or antennae with a small brush. Displays could be elicited within a minute or two after transferring the insect from the cold to the cage at room temperature, before its body temperature increased sufficiently to maintain flight. The responsiveness varied from specimen to specimen. Displays did not occur in response to the bats' echo-locating cries or to electronically synthesized ultrasonic pulses.

The sounds associated with the eyespot display can be separated into three components: grating sounds, low-intensity clicks and high-intensity clicks. Only the latter were studied in detail. Grating sounds, which are produced when the fore and hindwings rub against one another during a display (Haskell, 1956–7), have durations of about 100 msec and intensities of from 45 to 60 dB SPL. The frequency spectrum is very broad.

The second component consists of low-intensity clicks that are from 55 to 75 dB SPL in amplitude. Some occur randomly during the display while others apparently are associated with high-intensity clicks, occurring after a delay of from 10 to 150 msec.

The third sound component is a pair of high-intensity clicks, generated when the angle between the wings is from 30° to 60°, as the wings move forward and downward during a display. A typical click recorded from above the insect is shown in Fig. 1. Clicks have durations of from 30 to 100  $\mu$ sec, the interval between the clicks of a pair being typically from 10 to 100 msec. The waveform and intensity vary predictably according to the orientation of the animal. The initial phase is negative when recorded dorsally and positive when recorded ventrally. Clicks have maximum pressures of

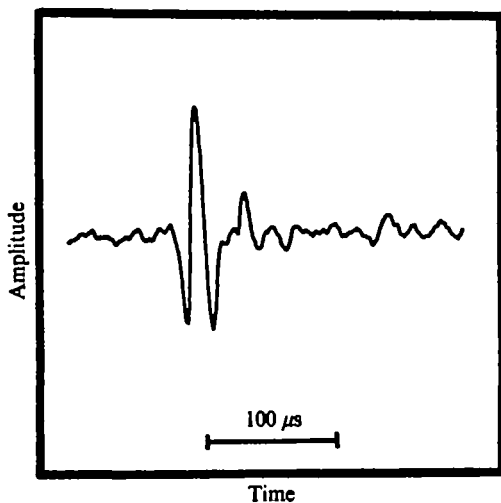


Fig. 1

Fig. 1. Waveform of a high-intensity click produced by a peacock butterfly. The amplitude of the click is about 100 dB SPL measured at 10 cm.

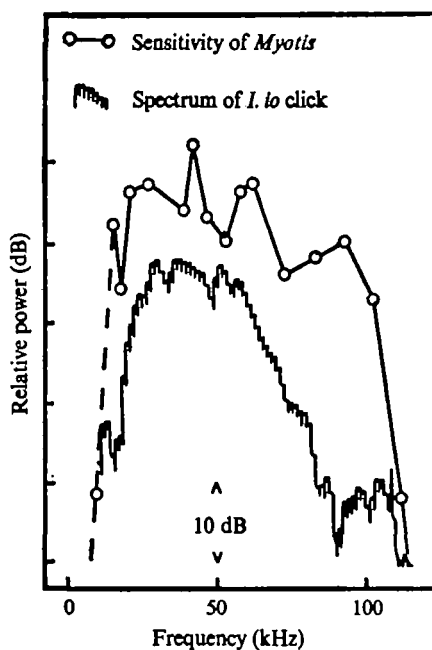


Fig. 2

Fig. 2. Power spectrum of a peacock butterfly (*Inachis io*) click (analysing bandwidth: 1 kHz) and auditory sensitivity of the little brown bat, *Myotis lucifugus* (redrawn from Dalland, 1965).

from 100 to 110 dB SPL when recorded perpendicular to the plane of the wing at a distance of 8 to 10 cm. The maximum energy lies between 30 and 60 kHz (Fig. 2), while the effective bandwidth is 45 kHz.

The site of click production was determined acoustically and by ablation. Clicks originated from the bases of the forewings, the mean distance between the source of each click in a pair being  $6.0 \pm 1.2$  mm ( $N = 27$ ). The physical distance between the wing bases is 6 mm. Ablation experiments show that the click-generating site is located in an area of wing membrane of about  $2 \text{ mm}^2$  between the costal and subcostal veins, where the former arches strongly at the wing base (Fig. 3). When this area is destroyed, by cutting it several times with fine iris scissors, the high-intensity clicks disappear or are reduced in amplitude by more than a hundredfold. The wing membrane in this region is stiff and mechanically bi-stable. By artificially moving the leading edge of the forewing against the tegula (a hollow cuticular structure at the anterior margin of the wing base (Fig. 3)) a click is produced when the membrane buckles dorsally. The artificially produced clicks have the same initial phase relationships and frequency spectra of normal clicks, but are about 10–20 dB less intense. A less intense click (60–70 dB SPL) occurs when the wing membrane returns to its resting position. We call this sound-producing structure the 'costal clicker'. This sound-producing structure in peacock butterflies has not previously been reported (see Dumortier, 1963 and Haskell, 1974). However, the butterfly *Ageronia*

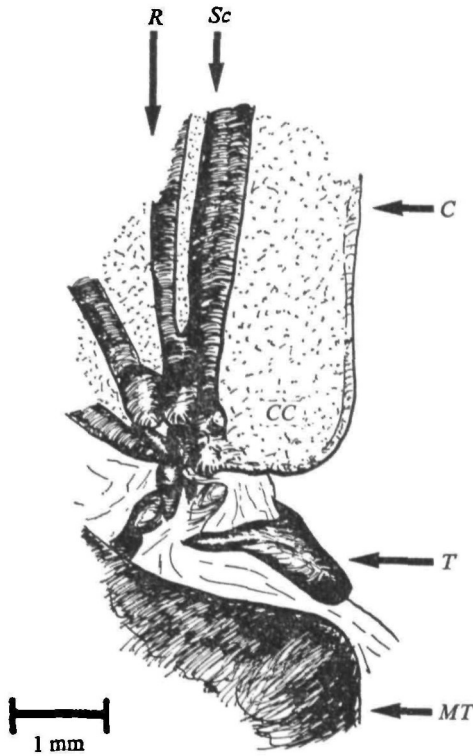


Fig. 3. Dorsal aspect of the forewing base in the peacock butterfly. The darker structures represent hard cuticle while stippled areas indicate wing membrane. *C*, costal wing vein; *CC*, 'costal clicker'; *MT*, anterior region of the mesothorax; *R*, radial wing vein; *Sc*, subcostal wing vein; *T*, tegula.

(Nymphalidae) produces audible clicks, but the mechanism has not been identified (Swihart, 1967). The costal clicker is probably activated when the leading edge of the forewing moves against the body during a display. Relative movements of the wing veins themselves cannot activate the costal clicker since clicks of normal intensity and duration persist after the wing veins are stabilized with a thick layer of wax.

The bats' response to displaying peacock butterflies was variable, consisting of audible screams, jumps, retreats, head jerks and pinna movements. The bats responded even when in their roosts where displaying butterflies could not be seen. Consequently, the bats responded to the acoustic rather than to the visual portion of the display. To decide which components of the display-coupled sounds elicited responses from the bats, we ablated both costal clickers of a peacock butterfly and presented it to a pipistrelle bat. Destroying the costal clickers does not interfere with the production of grating sounds. Displays by the operated insect did not elicit responses from the bat. We then presented to the bat an intact insect and one with the costal clickers ablated. As before, the bat did not react to a series of displays from the operated insect, but the moment the intact insect displayed, the bat tucked its head and remained motionless for half a minute. Consequently, the high-intensity clicks appear to be the sound component to which bats respond.

Bats behaved in similar manner to the displays of another hibernating nymphalid

butterfly, *Aglais urticae* L. Preliminary studies indicate that display-coupled clicks are produced in this species, but at an intensity 10–20 dB below those of *Inachis io*.

All three bats responded strongly on first encounters with displaying butterflies, and avoided further encounters. However, one pipistrelle bat readily attacked and ate butterflies only after having been exposed to many butterfly displays over a three-week period. Eating *I. io* and *A. urticae* did not affect the bat.

Since myomorph rodents are known to produce and respond to ultrasound (Sales & Pye, 1974), we investigated the response of house mice (*Mus musculus domesticus*) to *A. urticae* (*I. io* was not available). There was no avoidance behaviour or startle response from 5 mice to 90 encounters with 16 torpid insects. The attack was sometimes so swift that butterflies had little chance to display.

#### DISCUSSION

Eyespot displays of peacock butterflies retard or re-direct attacks by inexperienced passerine birds, but repeated exposures lead to habituation (Blest, 1957). Birds respond to the visual portion of the display and presumably cannot hear the display-coupled clicks since the frequency spectrum lies above the avian auditory range (Konishi, 1970). However, the auditory sensitivity of small mammals extends up into the ultrasonic range (Sales & Pye, 1974). Indeed, the energy spectrum of a click matches the auditory sensitivity of the vespertilionid bat, *Myotis lucifugus* (Fig. 2), as determined behaviourally (Dalland, 1965). Haskell (1956–7) suggested that the high-frequency components of the grating sounds (ultrasonic sounds were not recorded (personal communication)) may retard rodent predation. However, our preliminary studies show that the house mouse readily captures and eats *A. urticae*.

Clicks produced by peacock butterflies startle inexperienced bats, retard attacks, and thwart capture. Repeated exposures can lead to habituation, which may explain the observation that long-eared bats prey on hibernating nymphalids in nature (Roer, 1969). Thus, the effect of the clicks on bats appears analogous to the effect of the eyespot displays on birds. Ultrasonic clicks may, therefore, be considered the acoustic equivalent of an eyespot display. Since the details of bat–nymphalid butterfly interactions need further examination, the possibility remains that clicks announce the butterfly's distastefulness, as exemplified by arctiid moths (Dunning & Roeder, 1965; Dunning, 1968). The peacock butterfly, with its novel click-producing mechanism, can now be added to the list of insects able to foil bats (Roeder, 1967; Miller, 1975).

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