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WING-CLAPPING SOUNDS OF *EONYCTERIS SPELAEA* (PTEROPODIDAE) IN MALAYSIA

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Novick (1958) concluded that neither *Eonycteris robusta* nor *E. spelaea* is able to echolocate. D. Griffin (pers. comm.) and A. Grinnell tested a species of *Eonycteris* in New Guinea in 1969 and observed no signs of echolocation. Judging from photographic estimates of the nightly exodus, more than 4,000 *Eonycteris spelaea* roost in complete darkness in Batu Caves, 11 km NE of Kuala Lumpur, Malaysia (3°N, 102°E). In this cave, some bats must fly 300 m in complete darkness until they reach a small shaft of light. The wing-clapping, raindrop-like sound they produce while flying ceases with illumination of the cave at any time of day or night. The more than 5,000 bats that roost in lighted portions of the cave do not produce this sound. Bats netted from the dark portion of the cave and those netted in the naturally lighted portion of the cave produced the sound when observed in a dark room. *Eonycteris* also produces this sound when it flies in dark areas near *Oroxylum* or banana (*Musa*) trees (Gould, 1978). When these bats fly in dark caves, most fly at least 1 m away from the ceiling or walls.

It is unclear why Novick (1958) did not report this sound. It is possible that it does not occur in some populations or that he observed *Eonycteris* in partially lighted roost sites. Among 60 college students and several senior faculty at University of Malaya, none failed to recognize the association of wing-clapping sounds with darkness or their cessation with light. Such a crude sound could be used for echolocation, or the sound could simply be a concomitant of slowed flight. Swifts (*Apus apus*) and nightjars (*Caprimulgus europeaus*) both produce wing claps when their wing tips meet (Bundy, 1975); no function is known.

Over a period of 10 months (1974–1975), I brought more than 60 adult *Eonycteris* into the laboratory to determine experimentally the nature of the sound. Most bats were studied within a few hours of collection but some were kept for several days. Observations were conducted in an empty room (7.6 by 4.6 b 4.6 m) paneled with black plywood. The room could be rendered completely dark at midday but most observations were made at night. After 25 min of dark acclimation, light could not be detected even during the day.

As soon as a single *Eonycteris* flew in the dark room it produced sounds that resembled wings clapped together. As soon as I turned on a light, dim or bright, the sound stopped. Observations with an infrared viewer in the cave and in the room indicated that the sound (audible from about 30 m) was produced when bats were not near the ceiling or walls. Some bats flew near the ceiling of the room and cave. I painted the wings with slightly diluted white watercolor paint and could see marks left by some bats on the black ceiling of the experimental room.

To determine whether the wings touched one another, I painted one wing of 10 bats, five on the right and five on the left. When released in the dark, all bats marked the white paint onto the forearm and adjacent membrane of the unpainted wing. Little or no marking occurred when all bats flew in a lighted room.

I recorded flight sounds on a 18.75 cm/s Uher tape recorder; by slowing the tape speed it was possible to time the rate of wing clapping at four to seven per s. Suthers et al. (1971) reported a wing beat of about 10/s for *Phyllostomus hastatus*. A whistling sound was associated with wing-clapping; one of 20 bats produced only the whistle and no wing clapping. Wing clapping may persist a few seconds after the lights are turned on.

I presented 13 bats with two barriers of plywood boards 20.3 cm wide and 260 cm long, spaced 66.0 cm apart. Thin-walled, drawn-glass tubes were glued in their ears; tubes were plugged and unplugged with cotton, thus, the same animal was used as experimental and control. Touches and hits were counted as one and judged by listening as the bat flew in the dark room. There was no statistical difference ($P > 0.05$) between the two treatments in the number of times bats struck the wood. Bats with plugged tubes struck the boards slightly less often ($\bar{X} = 1.85$, median = 2, $SD = 1.97$, $n = 46$, range 0–10) than those with unplugged tubes ($\bar{X} = 2.76$, median = 2, $SD = 2.47$, $n = 38$, range 0–9; 140 trials).

In one series of experiments, I recorded only flight time. The bat was given a gentle toss in the dark room; the time until the bat fell to the floor or hung up was noted. Thirteen bats (different individuals from those used for the avoidance data) were released 82 times (41 plugged; 41 unplugged). In the 41 matched trials (the same bat served as control and experimental), 76% of the bats flew a shorter time with tubes plugged than unplugged. Bats also seemed more reluctant to fly if ears were plugged. Flight time differed by a factor of 2–5 times. For example, a bat that flew 3 s with plugged ears flew 10 s when its ears were unplugged; if the ears of the same bat were plugged again it reverted to a brief 3-s flight. The mean flight time for bats with plugged ears was 17.4 s (*SD* = 23; median = 9) and 28 s for those with unplugged ears (*SD* = 38, median = 17). These results indicate greater difficulty in flight by bats with plugged ears, suggesting possible reliance on echolocation.

Eonycteris spelaea of Batu Caves produced sounds by striking their wing membranes and forearms together; the sound is produced in dark situations (in caves while changing roosting places during the day, while departing after dusk, and while foraging on dark nights) but not in the light. If the sound is used for echolocation, it is a primitive system. *Eonycteris* can slow its flight in moderately dense foliage and when exiting from dark sections of the cave; deceleration may be associated with wing clapping. However, failure of bats with plugged tubes in their ears to strike barriers in the dark significantly more frequently renders conclusion about echolocation impossible. Possibly, the sound has no echolocation function but simply results from slowed flight. Decelerated flight may reduce the force with which bats collide with rocks or vegetation.

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LOAD CARRYING AND MANEUVERABILITY IN AN INSECTIVOROUS BAT: A TEST OF THE 5% "RULE" OF RADIO-TELEMETRY

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Radio-tracking studies of flying animals usually include the assumption that addition of a transmitter weighing 4–10% of the animal's body mass has a negligible effect on foraging behavior (Bradbury et al., 1979; Brander and Cochran, 1969). Criteria usually used to judge the success of these studies are whether the animal flies away without obvious difficulty and whether it survives beyond the expected life of the transmitter or after the transmitter has been shed. In many studies, only the first criterion is assessed and many animals simply disappear after attachment of the transmitter. Davis and Cockrum (1964) tested abilities of seven North American bat species to fly from the ground after loads of varying mass had been attached to their backs, and showed that some species could fly with loads of as much as 60% of their body mass. Caccamise and Heddin (1985) modified the aerodynamic theories developed by Pennycuick (1969) and Tucker (1973) to calculate the mass of a transmitter that produces a 5% increase in the power required for flight. Neither their model nor Davis and Cockrum's (1964) data indicate whether addition of a load affects behavior, or whether an increase of 5–10% in power required for flight is correlated with a deterioration in flight performance.

A bat's ability to maneuver is correlated significantly with its ability to turn tightly (Aldridge, 1985*a*).