Bat defence in lekking ghost swifts (*Hepialus humuli*), a moth without ultrasonic hearing

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The Hepialidae represents an early branch of the Lepidoptera, whose members lack the ultrasonic hearing and other obvious predator defence systems present in other extant moths. I observed lekking male ghost swifts, *Hepialus humuli*, being exploited by northern bats, *Eptesicus nilssonii*, over a hayfield in southern Sweden. Because the moth's display flight was restricted to a brief (30 min) period at dusk, they avoided most predators temporally but were exposed to early emerging aerial-hawking bats. Against these, they apparently employed 'acoustic crypsis', achieved by flying close (< 0.5 m) to the vegetation, thereby hiding from the bats among clutter (echoes returning from the background). Nevertheless, the predation risk for the displaying moth males was very high (20% per night), mainly because they sometimes left the safety of the vegetation. The lack of 'advanced' predator defence mechanisms in *H. humuli* requires alternative defence strategies, which, however, restrict the behavioural repertoire and still carry a high predation risk.

Keywords: arms race; *Eptesicus nilssonii*; sexual selection; predation; ultrasound

1. INTRODUCTION

The importance of echolocating bats as predators on moths over evolutionary time is illustrated by the presence of tympanic organs (ultrasound detectors) and associated evasive flight tactics among species in at least four Lepidoptera superfamilies (Noctuoidea, Geometroidea, Drepanoidea, Pyraloidea) (Spangler 1988; Fullard & Yack 1993). According to the scanty fossil record of the Lepidoptera, an order whose fossil record goes back to the early Mesozoic (Whalley 1986), the clades of hearing moths evolved only during the Eocene/Oligocene, after the appearance of bats. Nevertheless, these 'modern' groups of tympanate Lepidoptera dominate overwhelmingly the larger nocturnal moth fauna at present (Kristensen & Skalski 1998).

However, some presumably deaf Lepidoptera, which belong to clades that most likely pre-date the bats, such as the Hepialidae, still persist, and some of them are nocturnal or crepuscular. How do these 'living fossils' cope with bats? The Hepialidae are members of an ancient lepidopteran clade (Exoporia) that not only lacks ultrasonic hearing but also other predator defences such as aposematic/mimetic coloration and adaptations for manoeuvrable and erratic flight (the wings lack the frenulum–retinaculum coupling mechanism of most extant moths, and the fore- and hindwings therefore beat independently (Scoble 1992)).

Male ghost swifts, *Hepialus humuli*, are large (5–6 cm wingspan) and conspicuous (silvery white). They are typically seen during a period of *ca.* two weeks around the summer solstice (Svensson 1993), when they display in groups, performing a nearly stationary, hovering flight over open areas of herbaceous vegetation, attracting the attention of passing females both visually and with pheromones (Mallet 1984; Turner 1988). They restrict this lekking behaviour to a short (*ca.* 30 min) period at dusk, when reflectance from the green vegetation is fading out, and when the contrast between the wings and the background therefore is at a maximum (Andersson *et al.* 1998). This combines signal-quality maximization with temporal avoidance of diurnal insectivorous birds as well as late-flying, gleaning bats. At the same time, however, the display window coincides with the relatively early emergence of some aerial-hawking bats, which thus cannot be avoided (Jones & Rydell 1994; Andersson *et al.* 1998).

Accordingly, the purpose of this work was to investigate how the lekking *H. humuli* males deal with aerial-hawking bats, specifically the northern bat, *Eptesicus nilssonii*, a species which is known to prey heavily on these moths (Andersson *et al.* 1998).

2. MATERIALS AND METHODS

I observed northern bats exploiting a typical *H. humuli* lek at a 5000 m² uncut hayfield in southern Sweden (57° N) during eight evenings from 26 June to 4 July 1997. A 5 m × 12 m corner of the field, having 0.5–1 m high grass, was observed intensively from the edge (thus the moths were observed at a distance of 0–6 m) during the entire display periods (*ca.* 4 h of observation in total). The visual observations were aided by a bat detector (D-960, Pettersson Elektronik, Uppsala, Sweden) and a stop watch. The bats were probably from a known maternity colony of *E. nilssonii*, located *ca.* 200 m from the observation site (J. Rydell, unpublished observations). Their species identity was easily confirmed from their echolocation calls (Ahlén 1981). Visual observations were greatly facilitated by the relatively good light conditions at 57° N near the summer solstice.

The detailed behaviour of moths was sampled during 60 s of continuous focal observations of individuals ($n=37$), distributed among as many display sites as possible (within the field corner) to minimize the risk of pseudoreplication. The behaviour of the bats, including attacks on moths and the capture success, was quantified separately by observing the bats as they flew over the field. In addition, the number of displaying male moths in the field corner and the number of bats patrolling the whole field were counted (visually) every 5 min.

The moths' reaction to ultrasound was tested by using an electronic 'dog whistle', which produces a pure tone (26 kHz, 110 dB sound pressure level (SPL) re. 1 μPa at 10 cm (Rydell *et al.* 1997)) for as long as the button is pressed. The whistle was directed towards displaying *H. humuli* from a distance of 0.5–1 m, and the button was then pressed (manually) *ca.* 5–10 times in 1–2 s, to simulate an echolocating bat.

To get an indication of the energy content of the bats' prey and the size of the targets detected, eight *H. humuli* males were caught at a nearby lek (to avoid interfering with the lek under observation) and weighed on an electronic balance less than 1 h after capture. They were then spread and dried in a standard fashion and the wingspans were measured with callipers.

3. RESULTS

The display flights commenced at 23.05 h and ceased at 23.35 h (s.d.$=3$ and 7 min, $n=5$), agreeing almost exactly with earlier observations at nearby leks (Andersson *et al.* 1998). The daily maximum number of displaying *H. humuli* males in the 60 m^2 field corner varied between 10 and 37, and the density appeared to be similar throughout the field (*ca.* 100 m × 50 m). Each evening the lek was continuously patrolled from the height of 3–5 m by bats (*E. nilssonii*), usually 4–5 individuals at a time, the first of which arrived at the site within 1 min ($n=4$ evenings) after the appearance of the first moths. The bats caught on average 20% (s.d.$=6$%) of the displaying males (estimate based on three evenings with $n=20$, 27 and 31 displaying males, respectively), and in addition a few females. The predation pressure was thus very consistent from day to day, so the following data are pooled across evenings.

In search flight the bats used intense, strongly frequency-modulated echolocation pulses ending with a short, narrow-band 'tail' at *ca.* 30 kHz. Such calls are typical for this species, when it flies relatively low as reported here (Ahlén 1981; Rydell 1990, unpublished data). Attacks on moths were initiated from above (with one exception when the moth flew at *ca.* 3 m), and consisted of steep, almost vertical dives towards the ground. The attacks were always associated with a distinct increase in the echolocation pulse repetition rate, i.e. a terminal phase or 'feeding-buzz' (Griffin *et al.* 1960), strongly suggesting that the bats hunted by echolocation (and not by vision).

The bats' search times were long: 1.6 min for each capture attempt (34 attempts during 55 min of search flight). The moths spent 93% of the flight time ($n=37$ min of focal observation) in the 'gaps' between the relatively tall, panicle-bearing grass stems, but well above the blades, so that they were fully visible from above. However, 97% of the attacks from bats ($n=37$) occurred when the moths flew above the top of the panicles
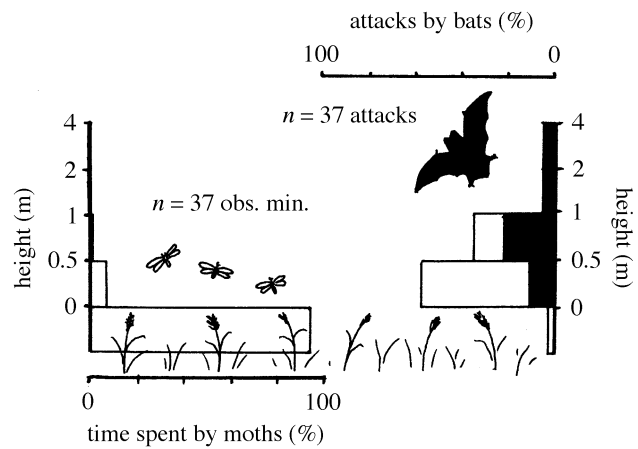

Figure 1. The flight height of displaying male ghost swifts, *Hepialus humuli*, over a hay field in relation to the top of the panicle-bearing grass stems (left bars) and the height where the displaying moths were attacked (right bars) and caught (black sections) by bats (*Eptesicus nilssonii*).

($\chi_1^2=59.0$, $p<0.0001$; figure 1). In addition, successful attacks occurred significantly higher than unsuccessful ones ($\chi_1^2=7.3$, $p<0.01$; figure 1).

Seventeen of 48 predation attempts (35%) were successful, as I saw the bat leaving the field with the moth in its mouth. In the other 31 cases, the attacked moth usually kept on flying, or, in two cases, it was knocked to the ground by the bat, but later resumed flight. The moths showed no evasive responses to bat attacks and none of 13 displaying males showed any response to the electronically produced ultrasound.

Moths occasionally left the safety between the grass stems and flew higher, exposing them to the bats, when they: (i) switched to a display position in another 'gap' (19 cases, 41% of the time); (ii) were displaced during a physical fight with another male (see Turner 1988) (17 cases, 35%); (iii) were carried away temporarily by gusts of wind (2 cases, 6%); and (iv) made vertical 'jumps' for unknown reasons (9 cases, 18%). The mean live weight of male moths was 283 mg (s.d.$=70$ mg, $n=8$) and the mean wingspan was 54 mm (s.d.$=4$ mm, $n=8$).

4. DISCUSSION

My observations of aerial-feeding bats attacking lekking male ghost swifts and my experiments with the dog whistle all substantiated the assumption that these moths do not hear echolocating bats. This does not mean, of course, that *H. humuli* has no defence against bats. On the contrary, the short display flights and the low flight positions of the males suggest that predation from bats could have been a major factor constraining the entire behavioural repertoire of the moths. They do not feed, and the males seem to restrict their flight to the lekking periods.

Accordingly, Lewis *et al.* (1993) suggested that, in general, nocturnal moths that lack ultrasonic hearing may be expected to compensate for their lack of ability to detect bats at a distance by consistently flying fast and/or erratically, so that they become hard to catch, and/or by staying near the ground, so that they are hard to detect

by echolocation (see also Chai & Srygley 1990; Srygley & Chai 1990). Lewis *et al.* (1993) also found evidence that North American species of moths behave according to these predictions. Furthermore, Morrill & Fullard (1991) suggested that deaf moths may be expected to minimize the time spent in the air, where they presumably are most exposed to bats (see also Cardone & Fullard 1988). The observations on *H. humuli* (Andersson *et al.* 1998; this study) largely corroborate all these hypotheses, with the exception that lekking *H. humuli* does not fly fast and erratically. This is probably because the Hepialidae lacks morphological adaptations for this form of predator defence (Scoble 1992).

The close correlation between the arrival time of the bats and the appearance of the first moths at the display site strongly suggests that the bats arrived to the site in order to exploit the moth lek in particular. The bats were only occasionally seen to engage in pursuit of other insects at this site.

The low attack rate (0.6 attempts per min as observed is less than 10% of the rate achieved in most other foraging situations (Rydell 1986)) suggests that the bats had difficulties detecting moths that stayed low (lower than 0.5 m above the panicles), or at least were reluctant to attack them. Reluctance to attack seems highly unlikely as an explanation for the low attack rate. There were no obstacles to manoeuvring above the grass blades except perhaps the panicles, which, however, seem unlikely to present any serious impediment. Instead, the bats were probably constrained by the clutter arising from the indistinctive background (see Kalko & Schnitzler 1993). Nevertheless, as confirmed by the close spatial and temporal association of moths and bats, the *H. humuli* males must still have been worth exploiting. The bats used on average 4.6 min of search (1.6 min/0.35) and *ca.* 1 min of handling for each moth that was caught (Rydell 1986). This means that each bat caught *ca.* six moths (together 1.7 g) during the time that the lek was in progress (*ca.* 30 min), i.e. one-third to one-quarter of the daily energy requirement (Kurta *et al.* 1989, 1990), assuming that the bats were pregnant and weighed 12 g each (Rydell 1989).

Whereas the male moths' low flight position provided acoustic crypsis from the bats, it also, presumably, meant that they were less visible to females (Mallet 1984; Andersson *et al.* 1998). If such a trade-off existed, the unexplained 'jumps' could have had the purpose of temporarily improving the visual signal that attracts females.

The observations may be of interest with regard to bat echolocation. *Eptesicus fuscus*, whose flight style and echolocation calls are very similar to those of *E. nilssonii* (J. Rydell, unpublished observations), can detect a 19 mm diameter square at 5 m (Kick 1982). Moreover, aerial-hawking bats (such as *Eptesicus* spp.) have been suggested to be able to exploit the Doppler-shifts produced by fluttering targets (Sum & Menne 1988) and to discriminate echoes with microsecond differences in arrival times (Simmons 1973). In the present case, the targets were 6 cm wide, i.e. three times larger than the disk used by Kick (1982), and there was up to 0.5 m between the target and the background, corresponding to almost a millisecond difference in echo arrival times. Therefore, at

3–5 m (the flight height of the bats), the detection of the moths would be expected to be a straightforward task. Because this was apparently not the case, it seems as if the performance of the bats was seriously constrained by clutter arising from the indistinctive, non-uniform and sometimes moving background.

The performance of wild bats in real foraging situations may thus be very different from what may be expected based on laboratory experiments. This discrepancy needs to be explored, particularly since the echolocation ability of bats has evolved in the wild and not in the laboratory (see also Barclay & Brigham 1994).

In conclusion, the lack of 'advanced' defence mechanisms, such as aposematism and/or ultrasonic hearing and evasive flight, usually present in large moths, requires alternative defence strategies in *H. humuli*. These strategies, however, permit less behavioural flexibility, and also carry a high risk of predation for the lekking males in particular.

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