Hearing and bat defence in geometrid winter moths

J. RYDELL[1], N. SKALS[2], A. SURLYKKE[2] AND M. SVENSSON[3]

[1] *Department of Zoology, University of Göteborg, Medicinaregatan 18, S-413 90 Göteborg, Sweden*
[2] *Centre for Sound Communication, Institute of Biology, Odense University, DK-5230 Odense M, Denmark*
[3] *Ecology Building, Lund University, Sölvegatan 37, S-223 62 Lund, Sweden*

SUMMARY

Audiograms and behavioural responses to ultrasound reveal that male geometrid winter moths (*Agriopis* and *Erannis* spp.; Ennominae, and *Alsophila aescularia*; Oenochrominae), which have large wings and a slow flight, have good, broadly tuned ultrasonic hearing with best frequencies at 25–40 kHz, coinciding with the frequencies used by most sympatric aerial-hawking bats. Ultrasonic pulses (27 kHz 110 dB at 1 m) delivered at distances of 1–12 m evoked consistent reactions of free flying, male *A. marginaria* in the lab as well as in the field; those at < 5 m resulted in the moth spiralling or diving towards the ground, those at 5–12 m resulted in one or several changes in the flight path, but did not end on the ground. The differential reaction probably reflects whether the moth is likely to have been detected by the bat or not. The micropterous (and flightless), and hence cryptic, females have strongly reduced tympanic organs and are virtually deaf. Sexual dimorphism in hearing and behavioural reactions to ultrasound reflect differential natural selection on males and females by bats. Natural selection on the hearing of the males thus seems to occur although they fly in late autumn and early spring, when bat activity is much reduced.

1. INTRODUCTION

Tympanic organs (ears) sensitive to ultrasound occur in several families of nocturnal Lepidoptera (see, for example, Scoble 1992). Detection of ultrasonic pulses, such as those emitted by foraging bats, elicits evasive flight manoeuvres, which help the moth to escape (Roeder 1967; Fullard 1988; Surlykke 1988). With few exceptions, that also involve intraspecific communication (see Spangler 1988 for a review), protection against bats seems to be the sole function of tympanic organs in moths; hence, insectivorous bats must have been a major selective force in moth evolution.

Efficient bat defence may be important for virtually all nocturnal moths although the defence strategies may vary from group to group. For example, the hawk moths (Sphingidae), most of which seem to be deaf (Scoble 1992), may perhaps acquire protection from bats by their size and powerful flight alone. On the other side of the spectrum are the mostly slow flying geometrids, including some 'winter' moths, the males of which maintain a slow, low energy flight even with body temperatures near freezing ($T_{\text{thorax}} < 1$ °C from T_{ambient}) thanks to a low wing loading (Heinrich & Mommsen 1985). For such moths, one may predict that bat defence based on hearing and evasive flight manoeuvres may be most essential. Female geometrid winter moths are either micropterous or apterous and hence flightless (Heppner 1991), and their tympanate organs show drastically reduced morphology (Heitmann 1934).

Noctuid moths that fly particularly early and late in the year show reduced hearing capacity compared to species that fly in summer, presumably because of relaxed selection pressure from bats during the cold season (Surlykke & Treat 1995). However, the noctuids in question (subfamily Cucullinae) maintain a high body temperature in flight and they fly fast (Heinrich 1993), thereby presumably gaining some protection from predators independently of their hearing. In contrast, we hypothesize that the relatively slow geometrids rely to a higher extent on their hearing based defence system. We thus predict that geometrids flying in the cold season may show a smaller reduction in their hearing capacity (compared to summer flying species; Roeder 1974; Surlykke & Filskov unpublished results) than noctuids that fly at the same time (Surlykke & Treat 1995).

Most previous work on hearing in moths has been done on relatively large bodied, fast flying species such as members of the Noctuidae, Notodontidae and Lymantridae. The geometrids have been much less studied (but see Roeder 1974), presumably because the delicate bodies of most species are more difficult to dissect and test physiologically. The hearing capacity of the flightless female 'winter' moths has never been examined.

2. MATERIALS AND METHODS

We investigated hearing ability in three species of closely related geometrids; *Erannis defoliaria* (Clerk 1759), *Agriopis aurantiaria* (Hübner 1799) and *A. marginaria* (Fabricius 1777), of the subfamily Ennominae, as well as in a more distantly related species *Alsophila aescularia* (Denis & Schiffermüller 1775) of the subfamily Oenochrominae. In addition, we studied the behavioural responses to ultrasound of male and female *A. marginaria*. The first two are among the last moths to hatch in the autumn, in October and November in southern Scandinavia, and their activity is usually stopped by the first heavy snow falls, marking the onset of winter. The latter two are among the first moths to appear in the spring, typically in March and April, usually while there is still some snow cover and the night temperature drops well below freezing on a regular basis. All four species are strictly nocturnal (Skinner 1984; Skou 1984).

Male *E. defoliaria* and *A. aurantiaria* were collected in an old deciduous woodland (mainly *Betula*, *Quercus*, *Tilia* and *Corylus*) near Ulricehamn in southern Sweden (57° 35′ N) 15–26 October 1995 either on lights or while they were sitting on the vegetation at night. Females of these species were collected by spraying a circle of shaving foam around tree trunks 1–1.5 m above the ground in daytime, later picking them as they emerged during the night and started to climb the trees, thus congregating below the foam. *A. aescularia* (males only) was collected in the same area between 31 March and 13 April 1996 mostly on lights. *A. marginaria* was collected in an old wood (*Fagus*, *Quercus* and *Corylus*) near Lund in southernmost Sweden (55° 40′ N) from 5–14 April 1996, by searching tree trunks for males and females. The moths were kept alive in a refrigerator at *ca.* 8 °C until they were processed 2–18 days after capture (2–10 days for females).

Freshly killed *A. aescularia* and *A. marginaria* males were weighed to the nearest 0.1 mg on an electronic balance. To estimate the wing areas, spread and dried moths, with the wings in the standard position, were put on millimetre graph paper, the outlines of the four wings were drawn and the squares covered by the outlines were counted. The area of the body was not included. Wing spans were measured between the wingtips of dried and spread specimens, using callipers.

Audiograms were recorded extracellularly from the tympanic nerve using a modification of Roeder's (1966) ventral approach. The moths were fastened ventral side up to a block of modelling clay with the wings clamped and spread open. The legs were removed at their coxa-trochanter junctions. The segments of the meso- and metathorax were separated using forceps and the coxae were fastened with needles to the clay. In these small moths, this was enough to expose the pterothoracic ganglion, the tympanic nerve, and the abdominal connective. In *A. aescularia*, the extracellular tungsten hook electrode was attached to the tympanic nerve. In the three other species the whole abdominal connective was hooked over the tip of the electrode. We thus recorded from the sensory cells of both ears at the same time, because we were unable to attach the electrode to one tympanic nerve alone. However, the activity from the four acoustic sensory cells of each ear was easily discernible also in the recordings from the connective.

The tympanic nerve activity was bandpass filtered (50 Hz to 10 Hz) and amplified (custom built amplifier) with a gain of 1000. The output was passed to an audio monitor and to an oscilloscope. The stimuli were 10 ms pulses (0.5 ms rise-fall time) repeated at 1 Hz. The stimuli were generated using a Hewlett-Packard function generator and a Panasonic Leaf Tweeter (EAS-10TH400B) loudspeaker. The output of the loudspeaker was calibrated using a 1/4′ Brüel & Kjaer (4135) microphone at the position of the moth and a 2606 Brüel & Kjaer amplifier. Frequencies between 5 kHz and 150 kHz were tested. The threshold was defined as the sound pressure level necessary to elicit 1–2 spikes in at least nine out of ten stimulations. Sound pressure levels are given in dB SPL (rms, re. 20 μPa). Following the determination of the whole audiogram, controls were made at 4–6 random frequencies. Preparations where the control threshold differed by more than 1–2 dB from the original values were excluded.

Behavioural responses of *A. marginaria* to ultrasound were tested in a flight room at Odense University, as well as in the old wood near Lund during 17–21 April 1996. We used an electronic dog whistle, which emitted a pure tone at 26 kHz (energies of the harmonics were attenuated 30 dB or more). The tone lasted as long as the whistle was activated and the sound pressure level was 110 dB SPL (rms) at 1 m (measured by a 1/4′ (4135) Brüel & Kjaer microphone). The repetition rate was controlled manually by pushing the button by a finger as rapidly as possible and, hence, was not controlled exactly.

In the flight room, five flying *A. marginaria* were tested at a distance of 1–3 m, and walking moths and flour beetles (controls) were tested at *ca.* 1 m. A series of 5–10 pulses were given in *ca.* 1–2 s, in an attempt to imitate the echolocation calls of an approaching bat. In the field tests, we estimated the distance between the sound source and the free flying male moths (*A. marginaria*) to the nearest metre by pacing. We also categorized the behaviour of the moths during the sound burst or immediately afterwards. We scored either a rapid dive (straight vertically) to the ground, a spiralling flight (not straight) to the ground, a rapid series of changes in the flight course ('zigzag flight') or a single change in the flight course. In the latter two cases, the moths always kept on flying rather than landing on the ground. In order to find the flying moths and observe their behaviour, a halogen head light (12 W) was used throughout the field tests, permitting observations of flying moths up to a distance of 25–30 m. In the field experiments we also made controls by pressing the opposite side of the dog whistle rather than the button, hence producing no sound, but otherwise following exactly the same procedure as in the tests. Obviously, the lamp could have influenced the behaviour of the moths. Therefore, we only tested moths which flew away from the lamp, apparently unattracted and undisturbed by it.

The sound pressure at 1 m from the dog whistle of 100 dB SPL corresponds roughly to the source level (sound level 0.1 m from the mouth) of the echolocation calls of an aerial-hawking bat searching for prey (Waters & Jones 1995), while 70 dB SPL, the dog whistle at *ca.* 25 m, roughly corresponds to the source level of a gleaning bat (Faure *et al.* 1990), assuming an atmospheric attenuation of 0.5 dB per metre and a spherical spreading loss of 6 dB per doubling of the distance (Lawrence & Simmons 1982).

3. RESULTS

(*a*) *Wing morphology*

In all four species the males have broad wings, characteristic of many geometrids, and they are very similar in general appearance (see, for example, Skinner 1984; Skou 1984). They are also similar in wing span, wing shape and weight (table 1). The very low wing loading results in the typically slow wing beat frequency and low flight speed, which we observed in the field.

(*b*) *Ultrasonic hearing ability*

The audiograms of males of each of the three species showed good hearing capacity in the ultrasonic range, with best frequencies (BF) at 25–40 kHz (figure 1). The males of the autumn species (*A. aurantiaria* and *E. defoliaria*) had BFs at 20–25 kHz. In *A. aurantiaria*, the BF was 24 ± 9 kHz (mean and s.d.), with a mean

Table 1. *Measurements of male geometrid winter moths (means and* S.D.*)*

species	fresh weight (mg)	wing span (mm)	wing area (mm^2)	wing loading (Nm^{-2})	*N*
A. aescularia	17.2 ± 3.3	32.7 ± 1.6	422 ± 42	4.05 ± 0.25	4
A. marginaria	16.9 ± 2.8	32.7 ± 1.9	400 ± 40	4.36 ± 1.15	6
E. defoliaria	—	36.3 ± 1.7	—	—	5
A. aurantiaria	—	34.8 ± 0.5	—	—	4

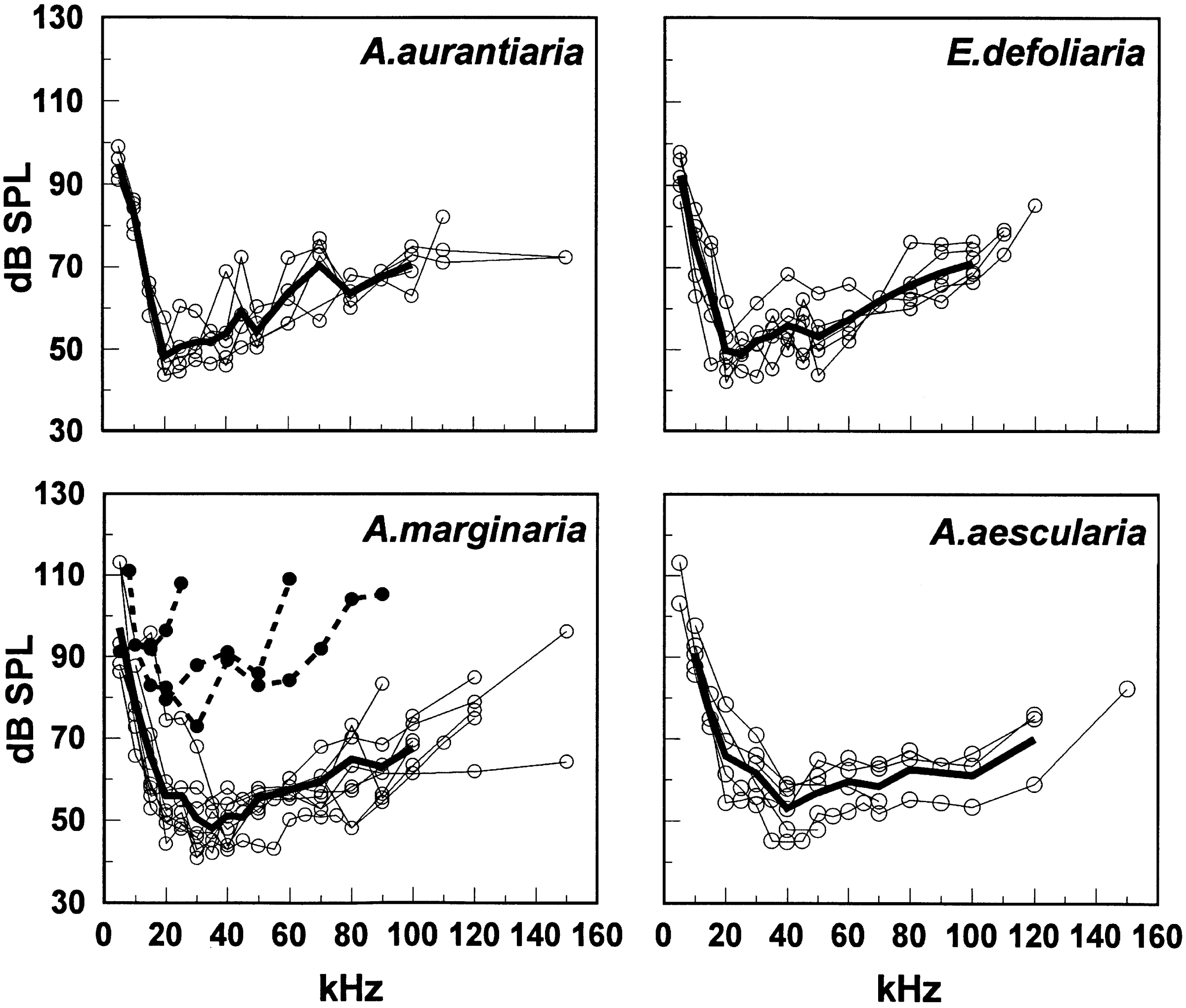

Figure 1. Audiograms of male Geometridae of the late autumn species (above) *Agriopis aurantiaria* ($N = 5$) and *Erannis defoliaria* ($N = 6$) and the early spring species (below) *Agriopis marginaria* ($N = 8$) (Ennominae) and *Alsophila aescularia* ($N = 5$) (Oenochrominae). The fat lines are species means for males. Open circles and the connecting lines represent measurements on individual males. In addition, values for three females of *A. marginaria* are shown by black dots connected by interrupted lines.

threshold of 47 dB SPL. The threshold increased steeply towards low frequencies and more slowly towards higher frequencies, thus reflecting broad tuning. At 100 kHz the threshold was only *ca.* 20 dB relative to the BF. Two individuals were tested at 150 kHz, where the threshold was around 70 dB SPL. *E. defoliaria* showed essentially the same characteristics as *A. aurantiaria* with BF at 28 ± 12 kHz, with a mean threshold of 49 dB SPL and a broadly tuned audiogram (figure 1).

The audiograms of the two spring species showed the same broad tuning, but significantly higher BF's than the autumn species ($p < 0.01$; Mann–Whitney *U*-test). Male *A. marginaria* had BF at 34 ± 7 kHz with a threshold around 50 dB SPL. At high frequencies, above *ca.* 90 kHz, the thresholds were very variable; in some specimens they could be determined up to 150 kHz and in others they exceeded the output of our system (*ca.* 104 dB SPL at 90 kHz). *A. aescularia* had BF at 48 ± 13 kHz and also showed a shallow increase in threshold towards higher frequencies (figure 1).

The morphology of the ear of *A. aescularia* also resembled that of *A. marginaria* in position and size (*ca.* 0.2 mm diameter). However, the tympanic nerve in *A. aescularia* had a very variable entrance to the central nervous system either on the ganglion or on either side of the abdominal connective, *ca.* 250 µm from the caudal end of the metathoracic ganglion. One specimen had a peculiar anatomy with the right tympanic nerve entering the ganglion and the left entering the connective.

While the ears of the males resemble those of other geometrids, the ears of the females are strongly reduced (Heitmann 1934; Scoble 1992) and difficult to see when observing the animal from the side. When moving the third leg into a rostral position, a little cup-like structure containing the tympanic organ could be seen. The cavity behind the ear was filled with air as in normal moth ears, but the tympanic membrane was opaque and thick compared to male membranes. The females were also more difficult to record from, and although we also tried with several individuals of the two autumn species, we only succeeded in obtaining audiograms from three females of the spring species *A. marginaria*. These audiograms showed large individual differences, but all showed very high thresholds at frequencies between 5 and 80 kHz. Outside this range, our system could not deliver enough sound pressure to exceed the threshold. In a fourth female *A. marginaria*, the threshold exceeded the output of our system at all frequencies, although we could elicit spikes in the tympanic nerve with the dog whistle at 30 cm (*ca.* 120 dB SPL at 27 kHz).

(*c*) *Behavioural responses to ultrasound-lab tests*

In the flight room, bursts of ultrasonic pulses were delivered five times towards each of five male *A. marginaria* at a distance of 1–3 m. All the 25 trials resulted in the moth instantaneously changing flight direction either horizontally or vertically apparently in response to the pulse. The change in flight direction was sometimes also followed by subsequent turns in the opposite direction, resulting in a zigzag flight. In some cases, the moth flew in a tight downward spiral and landed on the floor.

Three female *A. marginaria* walking on a vertical surface in the lab were also delivered five pulse trains each at a distance of *ca.* 1 m. All individuals consistently reacted by stopping instantaneously and remaining frozen for several seconds, usually until we forced them to move again by gently tickling them or blowing on them. To exclude the risk that the females actually stopped independently of the sound, we repeated the experiment five times with two females walking next to each other. In all cases, the two females froze simultaneously in the same way as the single females did. As a further control for the possibility that the moths actually reacted to something other than the sound, we tested three individual flour beetles (which are deaf), walking on the same surface. The beetles showed no noticeable reaction in any of the 15 trials.

The threshold for the behavioural response was estimated in two ways for one female. First, the maximum distance at which the dog whistle elicited the freezing response was 3–3.5 m, corresponding to a SPL at the moth of *ca.* 97 dB. Secondly, we placed the speaker we used in the electrophysiological tests 0.4 m from the female walking on a vertical surface of sound absorbing foam. In this way we could control the frequency and intensity of the stimulus, and we found behavioural thresholds of 83, 93 and 94 dB SPL at 10, 15 and 20 kHz, respectively.

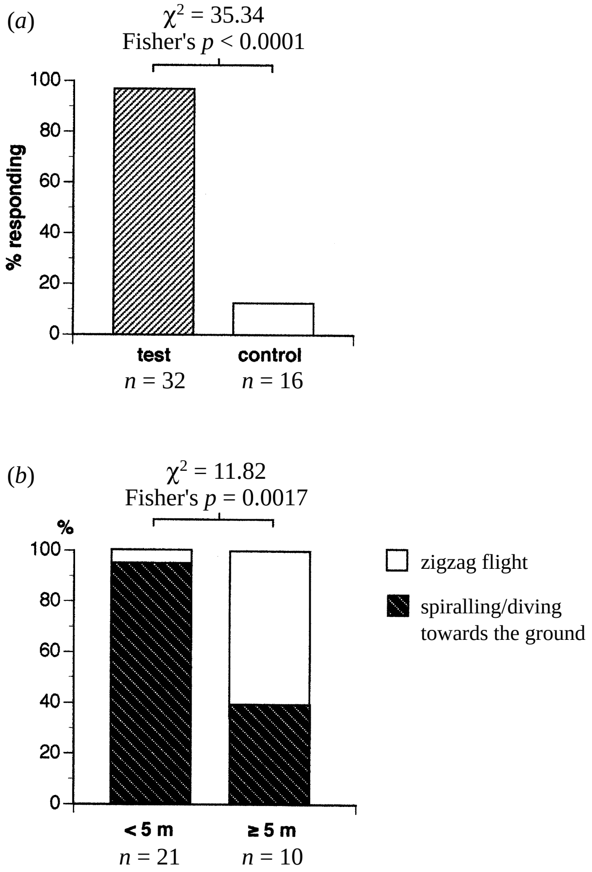

Figure 2. Behavioural responses of male *A. marginaria* exposed to bursts of ultrasound (26 kHz) in the field; (*a*) frequency of any response in test (sound; hatched) and control (no sound; white) experiments; (*b*) qualitative differences in the response in relation to the distance to the sound source (< 5 m and 5–12 m, respectively). The two categories of behaviour involve either one or several changes in the flight course (zigzag flight; white) or spiralling or diving to the ground (hatched).

(*d*) *Field experiments*

Tests on free flying male *A. marginaria* in the field confirmed and extended the results from the lab. The males reacted consistently, when exposed to bursts of ultrasonic pulses, at distances of 1–12 m. The frequency of response (96 %, $N = 32$) was significantly higher than in the control experiments (13 %, $N = 16$), where no sound was delivered (figure 2*a*). The moths responded with the same high frequency regardless of the distance to the sound source (1–12 m).

In the two cases (of 16) where the moths appeared to respond to the control experiment, the 'reaction' consisted of a simple change in the flight direction. This was in sharp contrast to the test experiments, where the response was not only consistent but also in most cases more dramatic, particularly when the sound was emitted at close range. The males reacted either by rapidly changing flight direction one or several times, resulting in a zigzag flight, or by diving rapidly or flying in a tight spiral, in the latter cases always ending on the ground. The type of behaviour changed significantly with the distance to the sound source, i.e. to the discerned amplitude. For example, 20 of 21 trials at < 5 m distance resulted in the moths spiralling or diving to the ground, and only one resulted in a zigzag flight that did not end on the ground. At distances of 5–12 m, however, only four of the ten trials resulted in spiralling or diving, and six in either a single change in the flight direction or zigzag flights. This difference in behaviour was highly significant (figure 2*b*).

Apart from the reaction to ultrasound in the lab, mentioned above, females in the field showed a tactile escape response; most of the individuals we caught or attempted to catch (about 100 altogether of three species) released their grip on the tree at the slightest touch. Several ended up in the leaf litter and disappeared, rather than falling into the collecting jar. We did not quantify this behaviour.

4. DISCUSSION

The hearing in the male winter moths was sharp and broadly tuned, encompassing the frequencies used by sympatric bats (Fullard 1988; Rydell *et al.* 1995), and it was similar to that of other geometrids which have been tested (Roeder 1974; A. Surlykke & M. Filskov, unpublished results). In the males, the hearing was similar in all the four species. The only obvious difference was that the autumn species had lower best frequencies (24–28 kHz) than the spring species (34–48 kHz), a difference for which we have no explanation at present. The weak auditory response of the female *A. marginaria* differed markedly from that of the males.

The males flying freely in the field reacted strongly and consistently to ultrasonic pulses delivered at 5 m or less, but showed a less dramatic response to pulses delivered further away. The repertoire of evasive responses could therefore be graded with the percieved intensity. Five metres is close to the distance at which an aerial-hawking bat can be expected to detect a moth of this size (Waters *et al.* 1995), although the moth will be able to detect the bat (or the dog whistle) much further away (*ca.* 25 m; calculated from the sensory thresholds). Hence, any prolonged reaction, such as spiralling or diving to the ground, to pulses emitted more than 5 m away, may be unneccessarily costly for the moth, since it is not yet at immediate risk. By a change in the flight course, the moth may still be able to get out of the bat's way and avoid being detected. It may also avoid landing on the ground and becoming exposed to terrestrial predators there. Hence, the qualitative change in the response observed at distances beyond 5 m appears highly adaptive.

The males' good hearing ability and sophisticated reactions to the ultrasonic bursts suggest that they maintain an appropriate defence system against aerial-hawking bats. There is no evidence that it has degenerated becase of partial protection from bats through allocation of the flight period early or late in the season, when bats may be less active, as appears to have been the case in some noctuids (Surlykke & Treat 1995). In the geometrids, which presumably gain no protection from their flight speed, a good hearing capacity may be essential even if the risk of encountering foraging bats is relatively low. In the area where the moths were caught for this study, aerial hawking bats such as *Eptesicus nilssonii* (Keyserling & Blasius 1839) are sometimes active in small numbers on mild evenings until late October and, in spring, from late March or early April (J. Rydell 1991, unpublished results). Hence, the geometrids we investigated must be exposed to foraging bats occasionally, although perhaps not on a regular basis.

The reduction of the wings and the hearing organs in the females may have taken place in concert (Heitmann 1934). A flying insect with a large surface area is more likely to be detected by an echolocating bat than a smaller and/or non-flying one. Therefore, once the wings have been reduced or lost, the moths have become cryptic, and the cost of reducing the ears as well may be small. In fact, a reduction of the ears may be highly beneficial particularly in geometrids, which have their ears situated on the abdomen, because losing the ears may provide additional space for eggs. This is in contrast to the Noctuidae, for example, where the ears are situated on the thorax (Scoble 1992). As with insects in general, female body size (or the space available for eggs) in geometrids is positively and almost linearly correlated with fecundity (Haukioja & Neuvonen 1985). Winter moths with flightless females are among the most abundant of all larger moths in Scandinavia and elsewhere at high latitudes, and their apparent success must at least in part be an indirect effect of the females' flightlessness, which permits increased reproductive capacity. This, in turn, may perhaps be evolutionarily feasible only at low densities of generalist predators and hyperparasites early and late in the season (Roff 1990; Sattler 1991).

For defence against vertebrate predators, female winter moths may have to rely on the response of falling to the ground when touched. The freezing reaction of the females could perhaps be used in the defence against gleaning bats, such as *Plecotus auritus* (L.), which forages on flightless prey and moths using low intensity echolocation in combination with other modes of perception (Anderson & Racey 1991). However, the females' remaining auditory capacity seems too reduced to allow them to detect the low intensity echolocation pulses used by gleaning bats, which have source levels of *ca.* 70–80 dB SPL (Faure *et al.* 1990). The behavioural thresholds of 85 to more than 95 dB SPL confirm the interpretation based on the physiological thresholds, namely that it is unlikely that hearing and reaction to ultrasound play any role in the females' defence against bats. Nevertheless, their freezing reaction was similar to that of many winged moth species being exposed to ultrasonic pulses while not in flight (Werner 1981).

In contrast to the female winter moths, female gypsy moths (*Lymantria dispar*; Lymantriidae), which have wings but seldom fly, showed no behavioural response at the sound intensities tested by Baker & Cardé (1978), and, since the ears are responsive, Cardone & Fullard (1988) concluded that there must be a central nervous decoupling of the motor (behavioural) output from the sensory input. However, our results from the geometrids lead to the opposite conclusion, namely that the evasive behaviour persists as long as there is any remaining hearing ability.

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