Sonic Hearing in a Diurnal Geometrid Moth, *Archiearis parthenias*, Temporally Isolated From Bats

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Many moths, including most Noctuoidea, Geometroidea, and Pyraloidea, possess ultrasound-sensitive ears, which probably evolved as a defense against echolocating bats [1]. Therefore we would expect moths that are isolated from bats geographically or temporally to be deaf or less sensitive than moths hunted by bats. However, studies of isolated moths living on remote islands or flying at winter have failed to show significant changes in threshold at the frequency of best sensitivity (BF) either in noctuids [2, 3, 4] or in geometrids [5], although some of the isolated noctuids have increased thresholds at frequencies above c. 40–60 kHz [3, 4]. Perhaps these moths retain good ultrasonic hearing because their form of temporal or geographic isolation is not effective enough. A recent report on degeneration of hearing in some dayflying moths (Dioptinae, Notodontidae) from Venezuela indicates that becoming diurnal may be an effective way of avoiding contact with bats [6]. Therefore we tested the hearing of the dayflying orange underwing, *Archiearis parthenias* (L.) (Archiearinae, Geometridae). We found that *A. parthenias*' hearing is unique for a moth. It is sensitive to sonic frequencies with a BF of 12 kHz. At bat-relevant frequencies (above 25 kHz) the hearing is degenerated such that *A. parthenias* is practically deaf above c. 60 kHz.

The majority of geometrid moths are nocturnal or crepuscular. However, all 12 species of the small subfamily Archiearinae, occurring in temperate areas and mountains, are diurnal. *A. parthenias* is distributed from Japan through Siberia to Western Europe and from Northern Scandinavia to the Alps. *A. parthenias* has a wingspan of 32–35 mm. The males typically fly very actively high among the tops of birch trees in bright sunshine in the early spring, whereas the females fly only little [7, 8]. In Sweden they fly in March–April, when few bats, if any, are active [9]. Thus, *A. parthenias* is isolated from bats both by its daily and annual times of flight activity.

Archiearinae have ears resembling those of other geometrids [10], placed at the base of the abdomen with four auditory sensory cells, A_{1-4}, in a scoloparium. The dendrites fold back on themselves after attaching to the tympanum. The scoloparium is therefore said to be inverse [8, 10]. All geometrid species tested have ears that are broadly tuned to ultrasonic frequencies with thresholds comparable to those of sympatric noctuids [5, 11].

We captured ten males by hand-netting near Ulricehamn (57° 30′N), Sweden, 10–16 April 1996. The males were flying in sunshine in a mixed coniferous forest with birch trees (*Betula* spp.). They were kept at 8°C until the following week, when they were tested at Odense University, Denmark.

Audiograms were determined as described earlier [5, 11]. Briefly, we recorded the tympanic nerve response to sound pulses by a tungsten hook electrode placed under the tympanic nerve, where it enters the abdominal connective just caudal to the metathoracic ganglion. We generated 10-ms stimulus pulses (0.5 ms rise/fall time) repeated at 0.5 Hz, using an HP 3314 function generator, an HP 8011A pulse generator, a Xelex amplifier, and a Technics Leaf Tweeter (EAS-10TH400B). Sound pressures are given in dB SPL (re 20 μPa rms). We tested frequencies of 3 and 4 kHz and from 5 to 100 kHz in 5-kHz steps. The threshold was defined as the sound pressure level necessary to elicit one or two spikes in at least nine of ten stimulations. Controls were performed at two or three frequencies after the whole audiogram was determined. Individuals were discarded if the controls differed by more than 2 dB. We obtained audiograms fulfilling the control criterion from five individuals (Fig. 1). All individuals were insensitive or deaf to most of the ultrasonic range tested. From 20 kHz the threshold increased steeply with increasing frequency and from 30 kHz the thresholds were significantly higher than in nocturnal geometrids (Fig. 1). Above 60–70 kHz the thresholds exceeded the maximum output of the system of c. 104 dB SPL. These thresholds were arbitrarily set to 110 dB SPL. In contrast, at sonic frequencies all tested moths were rather sensitive with a mean BF of 12 kHz (+6 kHz, $n=5$) and a mean threshold of 42+5 dB SPL at BF. From 15 kHz and below the threshold of *A. parthenias* is significantly lower than in other geometrids (Fig. 1).

The behavioral reactions to ultrasound were tested. We stimulated two free-flying individuals with trains of ultrasonic pulses (c. ten pulses) from an

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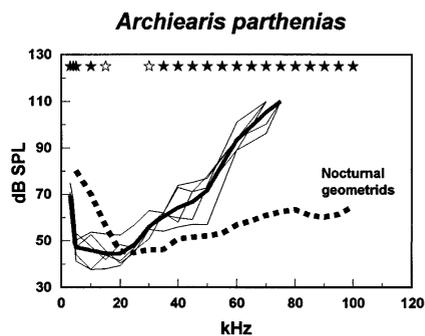All authors contributed equally to this paper.

Archiearis parthenias

Fig. 1. *Thin lines*, audiograms of five male *Archiearis parthenias; thick line,* mean audiogram. For comparison, the mean audiogram of 11 sympatric nocturnal species [5, 11] is shown (*dashed line*). *Stars*, the frequencies where the threshold of *A. parthenias* is significantly different from the nocturnal species (Mann-Whitney *U* test). *Filled stars, P<0.01; open stars, P<0.05*

electronic dog whistle (Pet Trainer). The whistle produces intense (110 dB SPL at 1 m) pure tones at 26 kHz (higher harmonics are more than 30 dB attenuated). Each pulse lasts as long as the whistle is activated. The two flying males were stimulated repeatedly from a distance of 1–2 m, hence with sound pressures exceeding their threshold by at least 50 dB. Neither of them showed any apparent reactions. Nor did the same stimuli from c. 1 m elicit any apparent reactions in moths sitting with the wings folded. Under identical conditions the same kind of stimulations elicited clear reactions in all individuals of a nocturnal geometrid species both when stationary and on the wing [5]. The results revealed clear differences in auditory characteristics between *A. parthenias* and other geometrids as well as other nocturnal moths studied. The audiogram with its low BF and insensitivity to high frequencies is mismatched to the sonar signals of the sympatric bats. Only one Scandinavian bat, *Nyctalus noctula*, emits main energy around 20 kHz. All the other species emit frequencies around or above 30 kHz. Since *A. parthenias* is not likely to encounter bats these

results confirm the hypothesis that bat predation is the primary force which has shaped and maintained the auditory characteristics and evasive behaviors of nocturnal moths. This conclusion is further corroborated by the lack of reaction to ultrasound of *A. parthenias*. The only other report of a comparable extreme reduction in high frequency sensitivity in moths is from some species of the diurnal notodontid subfamily Dioptinae (Noctuoidea) from Venezuela [6]. Our results from *A. parthenias* confirm that becoming diurnal seems to be a very effective escape from bats resulting in obvious degeneration of the ultrasonic hearing. However, even though *A. parthenias* resembles the diurnal dioptine moths in its high frequency deafness, it is unlike the dioptines at sonic frequencies. Those dioptine species, which show high frequency hearing loss, are also insensitive to low frequencies. Even at BF (around 10 kHz) the threshold exceeds 60 dB SPL [6]. In contrast, *A. parthenias* is just as sensitive at BF as are sympatric nocturnal geometrids at their respective BFs (Fig. 1). Consequently *A. parthenias* has improved its sensitivity to sonic frequencies compared to the ancestral form, which presumably is represented by nocturnal geometrids. This might indicate that the ears of *A. parthenias* are functional for some purpose other than bat detection, for example, intraspecific communication. Some temporally isolated moths, such as the diurnal noctuid *Hecatesia thyridion*, use their ears for sexual communication, but the tuning of their ears resembles that of non-isolated moths since the moths produce signals within the same frequency range as bat sonar sounds [12]. Alternatively, *A. parthenias* might use its ears for predator defense, for example, against small songbirds. However, we have no direct evidence supporting either of these suggestions. In addition, in flight the orange and black underwings make *A. parthenias* resemble some sympatric nymphalid butterflies,

i.e. the small tortoiseshell, *Aglais urticae* (L.). As a mimic of the aposematic *A. urticae, A. parthenias* may be sufficiently protected against bird predation. More data on the natural behavior of *A. parthenias* in the field are needed to reveal the functional significance of the sonic sensitivity of this moth ear.

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