

Observations on flight behavior and ultrasonic responses in moths (Lepidoptera: Erebidæ and Geometridæ) from Lapland

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Short Report

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Abstract

The absence of bats in high-latitude environments during summer, due to continuous daylight, provides a natural experiment to investigate the loss or persistence of acoustic defenses in moths. We conducted field observations and acoustic tests on Arctic moths (Lepidoptera: Erebidae: Arctiinae and Geometridae) in Finnish Lapland (Kilpisjärvi and Muonio) during July 2026, under 24-hour daylight. Individuals of *Diacrisia sannio*, *Arctia plantaginis* (Arctiinae), and several geometrid species were exposed to playback of bat echolocation calls and tactile stimulation, while their ultrasound emissions were recorded. None of the tested individuals produced ultrasonic clicks in response to any stimulus, suggesting loss or attenuation of acoustic defenses. We also performed observation on Arctic moths' flight behavior. Flight behavior of nocturnal geometrids differed markedly between periods of higher (03:00–21:00) and lower (21:00–03:00) solar altitude: during the night-like period, they flew slowly and unconcernedly, resembling chemically defended tropical species, despite lacking aposematic coloration. Diurnal insectivorous birds were active only during the higher solar altitude period and did not exploit these seemingly easy preys during the lower solar altitude period, despite sufficient light. These observations support the hypothesis that low predation pressure due to bat absence and limited bird activity has relaxed selection for acoustic and evasive defenses in Arctic moths. However, the preliminary nature of these findings calls for extended multi-season studies to confirm these patterns and explore their underlying mechanisms.

Introduction

The ecological relationship between insectivorous bats and moths represents one of the most studied examples of coevolution in predator-prey systems. Many moths, particularly those of the families Erebidae and Geometridae, have developed tympanal organs to detect bat echolocation pulses. Additionally, within Erebidae, the subfamily Arctiinae stands out by possessing tymbal organs on the metathorax, which produce defensive ultrasonic clicks (Fullard et al. 1979, Ratcliffe & Nydam 2008). In Geometridae the presence of tymbal organs has not been studied systematically, and thus far only a few confirmed records are known (e.g. Corcoran & Hristov 2014). These clicks may function as an aposematic signal, warning bats about the moth's toxicity, or as sonar interference (sonar jamming), or both (Corcoran et al. 2009). In environments where bats are absent, however, such acoustic defenses are expected to be lost or become redundant over evolutionary time, given the energetic cost of maintaining them (Fullard 1994). Studies in bat-free habitats, such as some islands in Polynesia (Fullard et al. 1982), and in the Canadian Arctic (Rydell et al. 2000) have demonstrated the loss or degeneration of acoustic startle responses in moths, supporting this hypothesis. Bat defense reactions have, however, been observed in Arctic Erebidae: Lymantriinae (Rydell et al. 2000).

During the Northern Hemisphere summer, the sun does not set north of the Arctic Circle. In the Kilpisjärvi (about 69°N) and Muonio (about 68°N) regions of Finnish Lapland, the photoperiod around the summer solstice consists of more than 50 days of 24 hours of continuous daylight, a condition that complicates the activity of insectivorous bats, which depend on darkness for foraging (Rydell et al. 2000). Kilpisjärvi

and Muonio do not have breeding bat populations, but there are a few records of the world's northernmost bat species *Eptesicus nilssonii* (Keyserling & Blasius 1839) in these areas (Tidenberg et al. 2019, FinBIF 2025). This scenario offers a "natural experiment" to investigate the persistence or loss of acoustic defenses in Arctic moths. This report describes field observations and tests of ultrasonic responses conducted during an expedition to the region, comparing the findings with behaviors of Neotropical (Brazil) and African (South Africa) moths.

Nocturnal moth species rarely fly undisturbed during daylight and fly rapidly to suitable hiding places, when disturbed, to avoid predation by diurnal predators. When moths of ancestral nocturnal lineages do make the transition to diurnalism, a transition is also observed in their mating behavior, flight mode, and defensive strategy in defense against diurnal predators (Staude 2008). This change from nocturnalism to diurnalism is most frequently observed in species that sequester secondary plant metabolites for their own chemical defenses during the larval stage, but also as an imago. The transition to diurnalism is also frequently accompanied by the prevalence of aposematic coloration as a warning signal to predators (Staude & Curle, 1997; Staude & Sihvonen, 2014). An additional objective of this expedition was to observe whether typical nocturnal moth species show any detectable differences in flight behavior under continuous daylight at these high latitudes, and how they may be exposed to diurnal predators for 24 hours.

Materials and Methods

The expedition was carried out in the Kilpisjärvi and Muonio region of Finnish Lapland during 4–11.7.2026, at the time of continuous daylight (Fig. 1). Individuals of Erebidæ and Geometridæ were tested for ultrasound production (Table 1, see Fig. 2a–c for examples).

Table 1

Erebidae and Geometridae species tested for ultrasound production. All study species have wide distributions, therefore there is likely gene flow between the northern and southern populations. We observed *Diacrisia sannio* in Muonio, which are potentially the northernmost records of the species in Finland (FinBIF 2025).

Classification	Species	Diel activity, Aposematism	Distribution	Specimens studied
Erebiidae: Arctiinae	<i>Arctia plantaginis</i>	diurnal, aposematic	Holarctic	1 m, 1 f
Erebiidae: Arctiinae	<i>Diacrisia sannio</i>	diurnal, aposematic	Palearctic	2m, 1 f
Geometridae: Larentiinae	<i>Xanthorhoe montanata</i>	nocturnal, non-aposematic	Palearctic	1 m
Geometridae: Larentiinae	<i>Rheumaptera undulata</i>	mainly nocturnal, partly diurnal, non-aposematic	Holarctic	1 f
Geometridae: Sterrhinae	<i>Scopula ternata</i>	nocturnal, non-aposematic	Palearctic	1 m
Geometridae: Ennominae	<i>Cabera pusaria</i>	nocturnal, non-aposematic	Palearctic	1 m

Ultrasonic emissions were monitored using appropriate recorders for bat-range frequencies (above 20 kHz). After immobilization, moth specimens were exposed to different stimuli, and their responses were recorded using a CM16/CMPA microphone. Stimuli consisted of (i) playback of *Myotis* bat attack calls, played near moth individuals immobilized by its wings (Fig. 2d-e), and (ii) gentle tactile stimulation using a fine brush and three different intensities.

To induce ultrasound production, the individuals were subjected to playback of bat attack calls, which were emitted by a speaker (AT100 Ultrasonic Transmitter, Binary Acoustic Tech) with a transmission capacity of 100 dB SPL, controlled by the BAT AR1xx software (Binary Acoustic Tech). The moths' responses to the ultrasonic stimuli were recorded with the CM16/CMPA microphone connected to an Avisoft UltraSoundGate 416H analog-to-digital converter (Avisoft Bioacoustics), enabling the recording and amplification of the insects' ultrasound emissions. In addition to the acoustic stimulus, recordings were also performed using tactile stimulation, aimed at simulating predation conditions. In this stage, a brush was used to touch the specimens at three distinct intensity levels. The sounds emitted during these tests were recorded and amplified following the same procedure described for the acoustic stimulus.

To observe qualitative flight behavior of typical nocturnal geometrid moths and their predators, we made several dedicated walks through various habitats in the Kilpisjärvi area over the five-day period covering all 24 hours of the day.

Results

None of the tested individuals, neither Arctiinae nor Geometridae, produced ultrasonic clicks in response to any of the stimuli applied.

During the Higher Solar Altitude (HSA, about 03:00–21:00), the aposematically colored male of *A. plantaginis* flew actively, rapidly and erratically during the mid-day sunshine, while the female was inactive and flew only when disturbed. In aposematically colored *D. sannio* males were flying semi-actively during the mid-day, and one male was observed flying at 21:00 when disturbed. Females concealed themselves among the vegetation. Neither species was observed flying actively during the night (Lower Solar Altitude, LSA about 21:00–03:00).

During the HSA, nocturnal geometrid moths flew only when disturbed, settling rapidly, except *Rheumaptera undulata* female, which was observed in the afternoon. During the LSA, typical nocturnal geometrid moths were abundantly flying in a seemingly unconcerned manner, without exhibiting rapid or erratic evasive behaviors. The observed behavior during HSA seems to agree with typical nocturnal geometrid moths that generally move quickly and soon conceal themselves when the vegetation they rest on is disturbed during the day. The observed behavior during the LSA seems to agree with typical nocturnal geometrid moths that flutter slowly over the vegetation at night. Diurnal moths (e.g. *Zygaena exulans*, *Sympistis lapponica*, *S. zetterstedtii*, *Anarata melanopa*)), and butterflies (e.g. *Euphydryas iduna*, *Erebia pandrose*, *Argiades optilete*) were actively flying as normal during the HSA but were not observed to fly at all during the LSA. Diurnal insectivorous birds (e. g. *Phoenicurus phoenicurus*, *Motacilla alba*, *Luscinia suecicus*, *Delichon urbica*) were active during the HSA and were observed feeding on insects during this time but were conspicuously not active during the LSA despite abundant light.

In summary these results indicate that the observed moths and their predators do not seem to markedly change their circadian rhythms at higher latitudes during the season where there is no darkness. Diurnal predators seem not to exploit easy prey during the LSA when typical nocturnal moths flutter slowly over the vegetation. This contrasts markedly with the authors' previous observations in Neotropical (Brazil) and sub-Saharan African (South Africa) regions, where nocturnal flying moths generally move quickly and soon conceal themselves when the vegetation they rest on is disturbed during the day. In tropical and subtropical regions, this fast and furtive flight behavior is characteristic of nocturnal species lacking chemical or aposematic defenses, while day flying species with such defenses (e.g. *Ctenuchina* wasp-like tiger moths) or mimetic aposematic color (i.e. *Cyllopoda* sp. (Geometridae); *Eucyane* sp. and *Hyalurga* sp. (Arctiinae: Pericopina)) may fly more slowly and "leisurely" (Chai 1996, Pinheiro 1996). The night active (LSA) Arctic geometrid moths observed in this study, although not displaying conspicuous aposematic coloration patterns, exhibited flight behavior similar to that of chemically defended tropical species.

Discussion

The absence of ultrasonic emission in the Arctiinae species tested suggests that acoustic defense against bats may have been lost or attenuated in these diurnal Arctic populations (Dowdy & Corner

2016, 2019). This result is consistent with the hypothesis that predation pressure exerted by bats is the primary selective factor maintaining tympanic organs and tymbals in moths (Fullard 1994). In high latitude and partially high-altitude Lapland, the bats are absent, and during the summer continuous daylight would hinder bat activity, as bats are exclusively nocturnal/crepuscular, creating an environment free of this predator. The functional loss of ultrasonic response in Arctic Arctiinae had been previously documented by Rydell et al. (2000), who found an absence of drop response to simulated bat calls in some species. The present study complements these findings by extending the lack of response to tactile stimuli and by including the family Geometridae, which, although generally lacking tymbals, may exhibit evasive behavioral responses in other regions. Rydell et al. (2000) noted that circumpolar *Psychophora sabini* (currently classified in genus *Xanthorhoe*), potentially the most cold-adapted geometrid (Downes 1964), walking on a surface froze at distances of at least 5–7 m from the bat sound source. However, two out of three individuals of this species (all males) did not respond in any way to the sound while in flight.

The "unconcerned" flight behavior observed in the nocturnal Arctic Geometridae moths support the hypothesis of low predation pressure. In tropical and subtropical environments, where predator diversity and abundance (bats, insectivorous birds, lizards, spiders) are high, moths that fly exposed and slowly would be quickly eliminated unless they possess chemical or aposematic defenses (Chai 1996). In the Arctic region, however, predator diversity is significantly lower, and their activity may be limited by the extreme climatic conditions during winter and the unusual photo period during summer. We also observed that most insectivorous birds were not active during approximately 21:00–03:00, further relaxing the predation pressure. The absence of intense selective pressure for rapid and furtive escape behaviors could therefore explain the seemingly "relaxed" behavior observed. Standardized experiments are required to test this hypothesis

It is worth noting that the Arctic geometrid moths observed did not display conspicuous aposematic coloration, suggesting that their unconcerned flight is not associated with a visual warning signal but rather with the general absence of predators that would warrant more cautious behavior. This observation contrasts with the pattern observed in tropical regions, where slow, exposed flight in non-aposematic species would be extremely costly (Pinheiro 1996).

In summary, the data reported here provide additional behavioral evidence for the hypothesis that low predation pressure in the Arctic environment, due to the absence of bats and foraging birds during the LSA, results in attenuation of acoustic and behavioral defenses in moths. Future investigations could examine whether auditory (tympanic) capacity has also been reduced in these populations through neurophysiological studies, and whether the behavioral pattern observed persists in other Arctic localities with similar photoperiods. Further, both examined arctiine species (*D. sannio* and *A. plantaginis*) have wide distribution ranges and they co-occur with bats for instance in Central and Southern Europe. The hearing and sound production on these species should be investigated in such areas.

The question arises why diurnal insectivorous birds, which were observed to be present at the study site and actively feeding on insects during the HSA do not seem to exploit the easy prey available during the LSA even though there is still sufficient light to see their prey. One possible explanation is that there has been insufficient evolutionary time for natural selection to favor individuals with shifted circadian activity rhythms that would allow them to forage during the LSA. Additionally, birds may require a period of inactivity for rest, which would constrain any such shift. Furthermore, the current post-glacial colonization of this region by both birds and moths is relatively recent (since the last ice age, ca. 10,000 years ago), and this interval may not have been long enough for the evolution of novel temporal foraging niches, despite the unique 24-hour daylight conditions combined with relatively mild temperatures (due to the Gulf Stream) that support a functional ecosystem of diverse vegetation, insect herbivores and vertebrate predators.

It seems that there has not been sufficient evolutionary time for local predators to adapt to the situation and exploit easy prey during the LSA. Therefore, the leisurely behavior of nocturnal geometrid moths has not been penalized by natural selection and has been maintained.

These observations are preliminary, as they were conducted over a short period. Further dedicated, structured observations over a longer period, preferably over several seasons, to support or refute these preliminary observations would greatly enhance our understanding of these unique phenomena.

Declarations

Author Contribution

SSM, HSS, RME and PS participated in the field expedition, carried out the field observations and wrote and reviewed the main manuscript textHSS, RME and PS collected the specimensSSM performed the ultrasound experimentsRME Took the photographs

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Figures



Figure 1

Observation sites of Arctic moths in Finnish Lapland. **1a.** Kilpisjärvi (about 69°N), showing mountain birch forest (*Betula pubescens* ssp. *czerepanovii*) in the foreground and Saana fjell in the background. Arrow shows the approximate location of photo 1b on top of the fjell. Photo from Wikipedia, CC BY. **1b.** Barren oroarctic alpine tundra on top of Saana fjell, about 1000 above sea level, 6.7.2026. Photo was taken around 1 am, showing the sun at its lowest point still well above horizon.

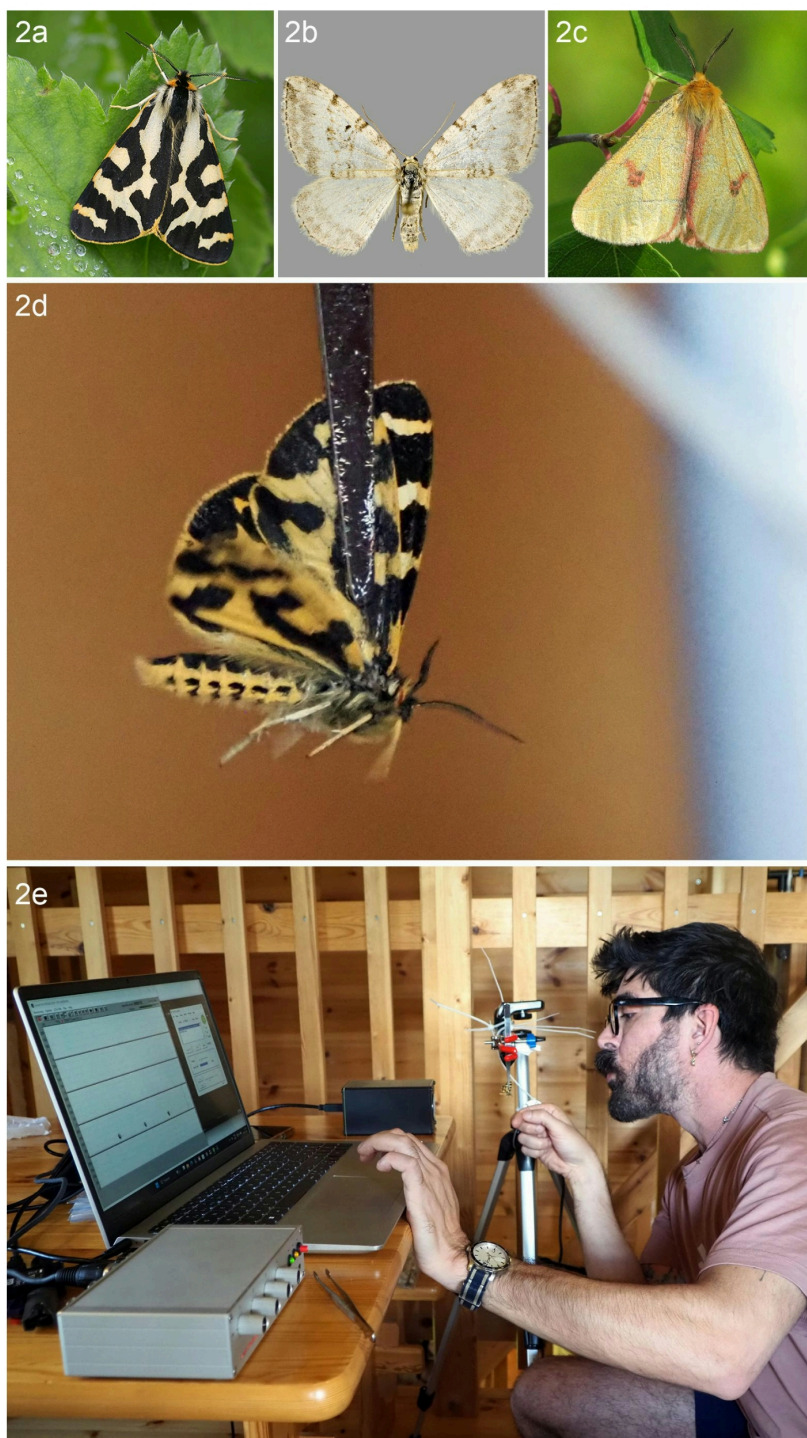


Figure 2

Selection of study moths observed in the Arctic Lapland and set-up for acoustic testing. **2a.** *Arctia plantaginis* male (CC BY, photo by Eino Ylönen from <https://laji.fi>). **2b.** *Xanthorhoe montanata* female (CC BY, photo by Pekka Malinen from <https://laji.fi>). **2c.** *Diacrisia sannio* male (CC BY, photo by J Lång from <https://laji.fi>). **2d.** *A. plantaginis* male. The specimen is held in tweezers to keep it in place, allowing for the study of its exposure to bat ultrasound and whether it produces ultrasound itself. **2e.** Ultrasound set-

up, showing Simeão de Souza Moraes, his laptop with accessories and the study specimen in front of the ultrasound speaker and microphone.