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Persistence of bat defence reactions in high Arctic moths (Lepidoptera)

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We investigated the bat defence reactions of three species of moths (*Gynaephora groenlandica*, *Gynaephora rossi* (Lymantriidae) and *Psychophora sabini* (Geometridae)) in the Canadian Arctic archipelago. Since these moths inhabit the Arctic tundra and, therefore, are most probably spatially isolated from bats, their hearing and associated defensive reactions are probably useless and would therefore be expected to disappear with ongoing adaptation to Arctic conditions. When exposed to bat-like ultrasound (26 kHz and 110 dB sound pressure level root mean square at 1 m) flying male *Gynaephora* spp. always reacted defensively by rapidly reversing their flight course. They could hear the sound and reacted at least 15–25 m away. *Psychophora sabini* walking on a surface froze at distances of at least 5–7 m from the 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. Hence, we found evidence of degeneration of bat defence reactions, i.e. adaptation to the bat-free environment, in *P. sabini* but not in *Gynaephora* spp. Some Arctic moths (*Gynaephora* spp.) still possess defensive reactions against bats, possibly because the selection pressure for the loss of the trait is such that it declines only very slowly (perhaps by genetic drift) and there may not have been enough time for the trait to disappear. One possible reason may be that Arctic moths have long generation times.

Keywords: adaptation; Canadian Arctic; Nunavut; predation; tundra; ultrasound

1. INTRODUCTION

An adaptation which is no longer selected for is expected to decline and eventually disappear, particularly if maintaining the trait is associated with a fitness cost. A well-cited example of the decline of such a useless trait comes from songbirds which are parasitized by cowbirds or cuckoos and which sometimes discriminate and reject the parasite eggs. This defensive behaviour is not maintained in areas where the parasites are absent or at times when they have decreased in abundance (Cruz & Wiley 1989; Davies & Brooke 1989; Soler & Møller 1990). However, changes in the frequency of their defensive behaviour have been observed over suspiciously short periods, a few years or decades, indicating that it may not be purely evolutionary (Brooke *et al.* 1998). Although rapid morphological evolution sometimes occurs in birds (Grant 1986), the effects of phenotypic flexibility and microevolution are apparently hard to separate.

We report here on the evolutionary fate of the bat defence systems of three species of high Arctic moths. The hearing organs and associated evasive reactions which normally serve to protect the moths from echolocating bats (Roeder 1967) are almost certainly useless for these insects, because there are no bats in or even near the high Arctic except very occasionally (Rydell *et al.* 1994). Their defensive reactions and hearing performance and perhaps also their ears may therefore be expected to degenerate and eventually disappear with ongoing adaptation to Arctic conditions or even by a random process (genetic drift). Since the moths do not feed and live only a few days in the adult stage (Ryan & Hergert 1977; Kukul &

Kevan 1994), it is very unlikely that behavioural flexibility or learning complicate the elimination of their bat defence reactions.

2. DISTRIBUTION AND CHARACTERISTICS OF THE SPECIES STUDIED

Moths of three species were used for this study: *Gynaephora groenlandica* (Wöcke, 1874) and *Gynaephora rossi* Curtis, 1835 (family Lymantriidae) and *Psychophora sabini* Kirby, 1824 (family Geometridae). *Gynaephora groenlandica* is 'known only from Greenland and from a few widely separated localities in the far northern Canadian Arctic' (Ferguson 1978, p. 20; see the distribution map in Danks (1986)), but there is also a single record from the North American mainland, from the British Mountains, north-western Yukon (Ferguson 1978). *Gynaephora rossi* is 'an inhabitant of the arctic tundra from Labrador to Alaska'. It then 'reappears southward at high elevations in the Rocky Mountains of Wyoming and Colorado, and above treeline on the highest mountains of the northern Appalachian system in Quebec, Maine and New Hampshire. It also occurs in Japan and Siberia' (Ferguson 1978, p. 18; see the distribution map in Danks (1986)). *Psychophora sabini* is circumpolar, occurring in the Arctic tundra and also at high elevations further south, e.g. in northernmost Scandinavia (Skou 1984). It 'may be considered the most fully adapted of all arctic Lepidoptera'. It is 'found alone at Isachsen, and at lake Hazen it emerges earliest in the season and has been taken at the summit of Mt. McGill' (Downes 1964, p. 288; see also Danks 1986).

Gynaephora spp. males are heavy-bodied, fast-flying moths which look like typical members of the family

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Table 1. *Place of origin of individual moths used in the field and laboratory tests*

(For the field tests n represents the number of tests performed (the number of individuals could have been smaller). For the laboratory tests n represents the number of individuals.)

locality	position	<i>G. groenlandica</i> / <i>G. rossi</i>	<i>P. sabini</i>
Melville Peninsula	67° 35' N, 81° 42' W	males, laboratory ($n = 2$) females, laboratory ($n = 1$)	—
Somerset Island	72° 55' N, 93° 27' W	males, field ($n = 5$) males, laboratory ($n = 10$) females, field ($n = 1$) females, laboratory ($n = 11$)	—
Cornwallis Island	74° 69' N, 94° 50' W	—	males, laboratory ($n = 1$)
Bathurst Island	75° 04' N, 98° 31' W	males, field ($n = 5$)	males, laboratory ($n = 2$)
King William Island	69° 07' N, 98° 55' W	males, field ($n = 19$)	—
Banks Island	71° 43' N, 123° 44' W	males, laboratory ($n = 1$)	—

Lymantriidae (mean live body mass \pm s.d. in *G. rossi* 125 ± 18 mg ($n = 10$) and in *G. groenlandica* 169 ± 18 mg ($n = 7$); recently emerged individuals were weighed on an electronic balance during this study). In both species, the females are much heavier than the males (*G. rossi* 556 ± 84 mg ($n = 11$) and *G. groenlandica* 658 ± 224 mg ($n = 2$)). Although *Gynaephora* spp. females have wings of almost normal size, they cannot fly with a load of eggs, a trait which is common among the Palaearctic and Nearctic lymantriids (Downes 1964). According to our observations and those of Ryan & Hergert (1977) and Kukal & Kevan (1987, 1994), the female starts the emission of pheromones and attracts males almost immediately after emergence, often before her wings are fully dry and while she is still sitting on the cocoon. Mating starts within seconds of the male's approach and oviposition usually takes place on the cocoon within a few hours. The process can be extended for several days under poor weather conditions. The males typically approach the female in fast, undulating flight, upwind 0.1–1 m above the ground. The low flight presumably facilitates negotiation of the usually strong wind on the tundra and it may also improve tracking of pheromone plumes which disperse less rapidly near the ground. The male sometimes lands a few metres from the female and makes the final approach by a walk on the ground. We observed that males of both species were attracted by females of both species. The adult moths do not feed and both males and females probably die within a day or so after mating and oviposition.

Psychophora sabini is a light-bodied (16 ± 2 mg ($n = 3$)), slow-flying moth much like a typical small geometrid. Some northern populations of this species show a tendency for wing reduction in the female, but males are always fully winged (Downes 1964).

3. MATERIAL AND METHODS

This work was performed during the Swedish/Canadian Tundra Northwest 1999 Expedition, based on the Canadian Coast Guard ice-breaker Louis S. StLaurent, which traversed the Canadian Arctic archipelago. Short (up to 36 h) helicopter-aided collecting visits were made to the tundra of several major islands and peninsulas. The material for the work presented here was collected at six of these sites between 6 and 29 July 1999 (table 1).

Cocoons with live pupae of *Gynaephora* spp. were systematically collected during each stop and virgin females were reared from these. Their reactions to ultrasound were first tested in the laboratory on board and sometimes also in the field. They were also used to attract males on subsequent stops. Most males of *Gynaephora* spp. were tested in the field as they flew towards pheromone-emitting females. *Psychophora sabini*, of which we obtained only three males, were only tested on board the ship, mainly because these moths were too infrequently (once) seen in flight on the tundra.

We found *G. groenlandica* but not *G. rossi* on Bathurst Island and Banks Island, while the situation was the opposite on Melville Peninsula. The two species occurred together on Somerset Island and King William Island, although *G. rossi* accounted for 80–90% of the individuals captured. Since the males tested in the field usually disappeared rapidly (see §4), we were often unable to confirm their species identity. Therefore, the field tests of the two species were analysed together.

The moths were exposed to short bursts of bat-like, ultrasonic pulses (around ten pulses in 1–2 s of a pure tone at 26 kHz and 110 dB sound pressure level root mean square, relative to 1 μ Pa, measured at 1 m; the second harmonic attenuated > 30 dB) from an artificial source (an electronic 'pet trainer' or dog whistle) (Rydell *et al.* 1997). Sound was produced when the button was pressed and, since this was done manually, the pulse repetition rate was not the same in all cases. Controls were made by pressing the opposite side of the whistle, thus producing no sound, but otherwise as in the tests. The sound generator is a very simple device but nevertheless triggers what seems to be normal evasive reactions in other moth species (Rydell *et al.* 1997).

The approximate distance between the moth and the sound source was paced out following each experiment in the field. Fixed distances were used in the laboratory, where each individual was tested at least five times at decreasing distances (25, 15, 10, 7, 5, 2, 1, 0.5 and 0.1 m). In this case each session involved five tests and the sessions were separated by at least 30 min in order to minimize the risk of habituation. The maximum distance at which the moth reacted in $> 50\%$ of the trials was considered to be its reaction threshold distance.

The field tests were performed in sunny but usually windy weather at temperatures of 10–15 °C and in places where the moths occurred naturally. The tests on board the ship were made indoors at 18–20 °C. Between tests, the moths were stored in permanent shade on the deck (0–10 °C). χ^2 -tests were Yates-corrected throughout.

Table 2. *The threshold distances at which individual Gynaephora spp. females stopped the emission of pheromones after being exposed to ultrasound*

species	site	female no.	threshold distance (m)
<i>G. rossi</i>	Somerset Island	1	2.0
		2	5.0
		3	0.5
		4	0.2
		5	2.0
		6	0.2
		7	1.0
		8	1.0
		9	1.0
	Melville Peninsula	10	2.0
		11	1.0
<i>G. groenlandica</i>	Somerset Island	12	0.0
		13	0.0

4. RESULTS

Male *Gynaephora* spp. exposed to ultrasound in the field (at distances of 1–15 m) as they approached pheromone-emitting females in low, upwind flight consistently (100%, $n = 29$; table 1) and instantaneously changed their flight direction to downwind, away from the sound source and the calling female. They usually disappeared rapidly at several metres altitude, aided by the wind. There was no indication that the evasive behaviour differed in any way between males at the three sites (Somerset Island, Bathurst Island and King William Island) or between the two species. This evasive behaviour was not observed in any other situation. One male (*G. groenlandica* from Banks Island) tested in the laboratory froze (i.e. stopped walking or fluttering the wings) at distances of 10, 20 and 25 m, but not at 30 m ($n = 2$ tests at each distance).

Female *Gynaephora* spp. were tested (in the laboratory) while emitting pheromones, as indicated by regular extension and retraction of the ovipositor and this behaviour was usually interrupted for a few seconds following the sound burst. Among the 11 *G. rossi* tested the threshold distance for reaction varied between 0.1 and 5 m, while the two *G. groenlandica* did not react at all, not even at 0.1 m from the sound source (table 2). We also performed controls for three of the females to ensure that the emission of pheromones did not stop for reasons other than the detection of ultrasound. This was indeed never the case ($n = 10, 22$ and 6 for females 1, 2 and 3, respectively; χ^2 -tests $p < 0.001$, $p < 0.001$ and $p = 0.05$). Hence, the females' response to ultrasound seems to be impaired (compared to the males) and highly variable and, in this case, there was a significant difference between the two species (Mann–Whitney U -test, $p = 0.026$).

The three male *P. sabini* (from Bathurst Island and Cornwallis Island) were tested as they flew or as they walked on a surface in the laboratory (distance to the sound source 1–7 m; table 3). Moths in flight usually did not react in any visible way to the sound bursts. However, one of the individuals from Bathurst Island (no. 3) performed a circling flight on four occasions (out of 23), which possibly occurred in response to the sound. When

walking on a surface and exposed to ultrasound all three *P. sabini* froze for a second or so before they resumed walking. However, they sometimes stopped walking even when not exposed to ultrasound (controls), but this occurred significantly less frequently compared to when they were exposed to ultrasound (table 3).

5. DISCUSSION

The bat defence reactions of the *Gynaephora* males were very consistent and comparable with those of other fast-flying nocturnal moths (e.g. Roeder 1967). They could hear the dog whistle at a distance of 15–25 m, which is within the range of thresholds observed among nocturnal moths inhabiting temperate latitudes with bats (e.g. Roeder 1966). The intensity emitted from the dog whistle is comparable to that of many species of echolocating insectivorous bats (Waters & Jones 1995) and the reaction distance observed for the moths in our experiments may therefore in rough terms be compared with those observed or predicted for moths exposed to real bat calls. Hence, we found no evidence that the defensive behaviour of *Gynaephora* males has degenerated in any way.

In contrast, the female *Gynaephora* spp. showed signs of a substantially degenerated anti-bat response compared to females of species which are normally exposed to bats (Acharya & McNeil 1998). *Gynaephora rossi* stopped the emission of pheromones when exposed to ultrasound at close range, indicating that it is their hearing which is impaired while their behavioural reaction remains relatively unchanged. However, as flightless females of many moth species, including lymantriids, show impaired hearing even in areas where bats are common (Cardone & Fullard 1988), the short reaction threshold distance in female *Gynaephora* is probably an effect of its flightlessness rather than of the absence of a selective factor (bats) in the Arctic.

The three *Psychophora* males were all responsive to the ultrasound when walking, as is normal in moths (Werner 1981), but two of them did not react at all while in flight. The third individual sometimes reacted by flying in a circle, a behaviour which is perhaps a remnant of the spiralling, downward flight shown by some other geometrids when exposed to bat-like sound at close range (Rydell *et al.* 1997). Hence, in this species, '... the most fully adapted of all arctic Lepidoptera ...' (Downes 1964, p. 288), we found evidence of degeneration or disappearance of evasive flight behaviour. Nevertheless, all three individuals were still able to hear the ultrasound and reacted appropriately while walking.

The hearing organs may compete for space with the ovaries in some female moths and for these it seems clear that the possession of a hearing system is associated with a considerable fitness cost (Rydell *et al.* 1997). However, it is not clear whether a similar argument can be made for males, although it seems likely that their hearing organs may restrict the space available for flight muscles (Byers 1969), which are important for flight performance and heat production (Heinrich 1993). A tympanic organ (a cleft with a thin membrane) may also be disadvantageous if it is vulnerable to infestation by parasites, although this may not necessarily be a problem for *Gynaephora*, which spend only a few days in the adult stage.

Table 3. *Frequency of reactions of P. sabini males after exposure to ultrasound*

(The distance from the sound source to walking moths was 1–7 m and to flying ones 1–2 m. An asterisk indicates that this individual moth reacted by performing a circling (spiralling) flight. It did not dive towards the floor, however, as might have been expected (Rydell *et al.* 1997).)

site	male number	walking		flying	
		freezing	no reaction	diving	no reaction
Cornwallis Island	1, test	25	0	0	8
Bathurst Island	2, test	11	0)	0	10
	2, control	3	9)		
	3, test	8	0)	0 (4*)	19
	3, control	3	20)		

A reduced hearing capacity has been observed in temperate and tropical moth species which have become isolated from bats temporarily (Fullard *et al.* 1998) or geographically (Fullard 1994). However, Surlykke (1986) found no evidence of reduced hearing in moths from the Faroe Islands, although bats are absent. She suggested that their hearing may be maintained by gene flow from mainland Europe, where conspecific moth populations are exposed to bats. Alternatively, the time since the moths in question immigrated to these islands may not have been long enough for evolution to have had any impact on their hearing (Surlykke 1986). In contrast, moths endemic to the bat-free, tropical island of Tahiti do show impaired hearing (Fullard 1994). Whether their defensive reactions persisted or not was not investigated in either of these cases.

An important question remaining is whether the moth populations that we studied are entirely isolated from bats or not and, hence, whether the implicit assumption that there is no gene flow between areas with bats and the high Arctic can be justified. *Gynaephora groenlandica* is endemic to the tundra of Greenland and Arctic Canada and, to our knowledge, only one bat has ever been reported from this area; a hoary bat (*Lasiurus cinereus*) was found at Southampton Island (64° N) in 1942 (Hitchcock 1943). The other two species (*G. rossi* and *P. sabini*) have distributions which also include the Arctic coasts of Alaska and Russia and high Alpine (tundra-like) areas of some mountains further south. We cannot be certain that gene flow from these peripheral populations to those of the high Arctic does not exist, although for this to have any impact would require (i) that the peripheral populations are subject to natural selection from bats, and (ii) that there is immigration from these populations to the high Arctic. That the male *G. groenlandica* (the only *Gynaephora* species found on Bathurst Island) behaved identically compared to *G. rossi* (the commonest species on Somerset and King William Islands) does not support this. Bats usually avoid the tundra as well as treeless Alpine areas, at least at higher latitudes (Rydell *et al.* 1994). Gene flow between the mainland and the Canadian Arctic islands must either be maintained by the immature stages (perhaps by the wind carrying larvae or cocoons in the air or over the sea ice) or, because the females are flightless, by the males alone.

Our results will also be difficult to interpret if the species studied engage in acoustic communication and, hence, use their ears for this purpose. However, auditory communication is relatively uncommon in moths, as are sound-producing organs. Neither has been observed in any member of the Geometridae, one of the families which we used in this study (Conner 1999). The presence of abdominal tymbal organs in some male Lymantriidae suggests that these species may communicate acoustically (Dall'Asta 1988). However, two lines of evidence suggest that this is not the case in *Gynaephora* spp. First, male tymbal organs are absent in all lymantriid species investigated with weakly flying or flightless females (Dall'Asta 1988), although *Gynaephora* spp. seem to be unknown with respect to this. Second, we observed a highly variable threshold distance among the females, which probably reflected a highly variable hearing capacity. This in turn indicates that there is little or no selection pressure which maintains hearing in females.

According to Strathdee & Bale (1998), 'Much of the research on Arctic insects has been focused on' ... 'identification of the adaptive mechanisms that enable a relatively small number of species to survive in such a stressful climate' (p. 86). The implicit assumption of this is that prosperity in Arctic environments requires adaptations to the particular conditions prevailing there (McAlpine 1964). However, our results indicate that some insects (including *Gynaephora* spp.) survive and reproduce in the Arctic essentially without being extensively adapted to their habitat. Instead they may depend on pre-adaptations, i.e. traits which evolved elsewhere and which thus became established before the species invaded the Arctic. Adaptation is usually a slow biological process and, as suggested by Surlykke (1986), it seems possible that the time since the moths invaded the Arctic has not been long enough for adaptation to occur (Downes 1962, 1964; Strathdee & Bale 1998).

Indeed, a slower rate of evolution may be expected in Arctic insects than in tropical ones because growth and maturity takes more time. For example, *G. groenlandica* in Arctic Canada needs up to 14 years or more to develop from egg to imago (Kukal & Kevan 1987, 1994). Such long generation times may perhaps explain why this species seems to be less extensively adapted to its habitat than are those of the tropical island of Tahiti.

It is not known how long *Gynaephora* spp. and *P. sabini* have inhabited the Arctic, although their wide Arctic distribution and their virtual absence from temperate regions suggest that the invasion was not recent. Hence, our results suggest that useless anti-predator adaptations disappear over long time-spans and not within a few years or decades of relaxed selection pressure. It may of course be different if behavioural flexibility or learning is involved, as was probably the case in the bird examples cited in § 1 (Brooke *et al.* 1998) or in animals with short generation times.

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