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Author(s): Jens Rydell and Winston C. Lancaster

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Flight and thermoregulation in moths were shaped by predation from bats

Jens Rydell and Winston C. Lancaster

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Most larger nocturnal moths (“macrolepidoptera”) are equipped with ultrasonic tympanic organs (ears), which give them a considerable survival advantage in encounters with echolocating bats. However, 4.2% of the Scandinavian species lack such organs, and are presumably deaf. Our results show that the earless species are larger and have higher wing loadings than the tympanate forms. They also fly with higher body temperatures. They are thus adapted for fast and erratic flight, and may represent an alternative evolutionary pathway to efficient bat defence, but one that is energetically more demanding. We suggest that the tympanic organs in nocturnal moths were key innovations that “released” their bearers from the energetic constraints imposed by a high flight body temperature, necessary to avoid bats, and probably set the stage for subsequent adaptive radiation of slow flying forms.

J. Rydell and W. C. Lancaster, Dept of Zoology, Göteborg Univ., Box 463, SE-405 30 Göteborg, Sweden (jens.rydell@zool.gu.se).

Echolocating bats have been a major selective agent in the evolution of moths (Lepidoptera), as judged by the presence of ultrasonic tympanic organs (ears) in at least five major superfamilies, namely the Pyraloidea, Geometroidea, Drepanoidea, Uranoidea and Noctuoidea (Eggers 1919, Roeder 1967, Spangler 1988). In addition there are non-tympanic hearing organs in some Sphingoidea (Roeder et al. 1970). These moth ears are tuned to the ultrasonic biosonar frequencies used by bats (Fullard 1988) and provide the moth with an early warning system of considerable survival advantage (Dunning et al. 1992, Pavey and Burwell 1998).

Some moths (Lepidoptera) typically fly with a very high thoracic temperature (T_{th} , near 40°C; Bartholomew and Heinrich 1973, Heinrich and Casey 1973, Casey and Joos 1983), while others work at T_{th} near ambient, even when the latter approaches freezing (Heinrich and Mommsen 1985). Thoracic temperature is closely correlated with wing loading (mass \times gravity/wing area) in moths (Bartholomew and Heinrich 1973, Casey and Joos 1983) and because wing loading is generally a good predictor of flight speed (Norberg

1990), warm-bodied moths presumably fly much faster than cold-bodied ones.

Why such a broad range of T_{th} 's and wing loadings have evolved in moths is unclear, but the observation that non-tympanate (earless), nocturnal species typically fly more erratically than tympanate ones (Lewis et al. 1993) suggests that bat predation might be partly responsible. It seems possible that fast and erratic flight, which requires high metabolism and thus probably a high T_{th} (Chai and Srygley 1990), may have evolved in moths as an alternative or a complement to ultrasonic hearing as defence against bats.

We examined the prediction that non-tympanate moths have higher wing loading and higher T_{th} than tympanate moths. We concentrated on large forms, the “macrolepidoptera” and larger (wingspan > 15 mm) Pyralidae (which usually are treated among the “microlepidoptera”), but excluded the butterflies and also the Zygaenidae and Sesiidae. The members of the latter two families have predator defence systems based on aposematism and mimicry, respectively, and are considered exclusively diurnal (Heath and Emmet 1985,

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Scoble 1992). Omitting these, tympanate and non-tympanate macrolepidoptera have roughly equivalent diversity at higher taxonomic levels and are each represented by eight families in Scandinavia. At a lower taxonomic level, however, the non-tympanate families are much less diverse, comprising only 4.2% of the species ($N = 1093$; Table 1).

Materials and methods

One to five individuals of each species were caught during the night using Hg-light or hand netting in various places and habitats (mainly taiga, deciduous woodland, unimproved pasture and coastal habitats), in southern Sweden (56–58°N) between April and October 1996–1997. The moths were killed with ethyl acetate, weighed to the nearest 0.1 mg, pinned, and spread in the standard way (with the dorsal of the forewings perpendicular to the body). We included every species that we caught with the exception that we restricted ourselves to one species per genus to avoid the disproportionate impact of multi-species genera. However, for the family Hepialidae, which is represented by only one genus in our area, we included the five species that were available. We restricted the analysis to males, which typically fly more than females (Svensson 1996), and therefore probably are more affected by bat predation (Acharya 1995).

Wing areas of the dried specimens were measured digitally (Space Image Software, Silicon Graphics). We excluded the head, body and small area of overlap between the fore- and hindwing from “wing area”, but included the wing fringes (Norberg 1972). For some

small families we increased the number of species by using dried specimens from JR’s private collection (2 Hepialidae, 1 Cossidae, 1 Limacodidae, 1 Lasiocampidae, 2 Lymantriidae; 1–4 individuals per species). These were weighed and their wing areas were determined as for the fresh individuals. Dry mass was then converted to “fresh mass” using a conversion factor (1/0.36) that was obtained by comparing dry mass to fresh mass for 20 other species (1–3 individuals per species). The ratio of dry to fresh mass was consistent among all the 20 species (C.V. = 12.6%) and not significantly correlated with original (fresh) mass ($r = 0.184$, $N = 20$, $P = 0.44$).

Thoracic temperature in flight was obtained to the nearest 0.1°C by using Heinrich’s “grab and stab” method (Heinrich 1993; thermoprobe diameter 0.4 mm) on moths coming to a Hg-light. Stabbed specimens were discarded and not used for other measurements.

Results

Mean wing loading was significantly higher in earless families than in tympanate ones (mean and S.D.: 4.3 ± 2.4 and 2.1 ± 1.3 N m⁻², respectively, $N = 8$ and 8; $t = 2.27$, $P = 0.037$) and the earless species were also significantly larger (47.2 ± 2.4 and 32.3 ± 5.9 mm wingspan; $t = 2.71$, $P = 0.017$; Table 1).

Wing loadings near 1 N m⁻² are typical of the tympanate families Pyralidae, Geometridae, Arctiidae and Herminiidae and also occur with lower frequency in all the other tympanate families except the Notodontidae. However, such low wing loadings were not found in any species of the earless families. The lowest wing loadings among earless moths were found in the

Table 1. Taxonomic diversity, wing span and wing loading in families of Scandinavian “macrolepidoptera” and larger Pyralidae (excluding butterflies and two families of exclusively diurnal moths). “No. of species in Scandinavia” is from Gustafsson (1994). N is the number of species measured (the mean of 1–5 individuals per species, all males).

Superfamily	Family	No. of species in Scandinavia	Wing span (mm)		Wing loading (N m ⁻²)		N
			Mean	S.D.	Mean	S.D.	
<i>Earless</i>							
Hepialoidea	Hepialidae	6	34.2	11.6	3.41	0.82	5
Cossoidea	Cossidae	4	50.3	16.9	8.88	2.19	3
Zygaenoidea	Limacodidae	2	23.0	–	2.42	–	1
Bombycoidea	Lasiocampidae	14	39.6	10.8	3.97	0.55	8
	Lemoniidae	1	47.1	–	2.87	–	1
	Saturniidae	2	58.0	–	1.80	–	1
	Endromidae	1	59.3	–	4.08	–	1
Sphingoidea	Sphingidae	16	66.0	13.3	7.06	3.99	5
<i>Tympanate</i>							
Pyraloidea	Pyralidae	204	24.1	4.5	1.00	0.33	14
Drepanoidea	Drepanidae	16	30.0	7.0	1.92	1.20	8
Geometroidea	Geometridae	323	26.6	7.0	0.96	0.55	55
Noctuoidea	Notodontidae	29	41.8	9.1	4.32	2.16	11
	Lymantriidae	13	36.1	6.0	2.35	1.52	6
	Arctiidae	39	34.2	13.7	1.59	1.44	8
	Herminiidae	9	29.2	2.2	0.80	0.13	2
	Noctuidae	414	36.5	7.5	3.63	1.36	56

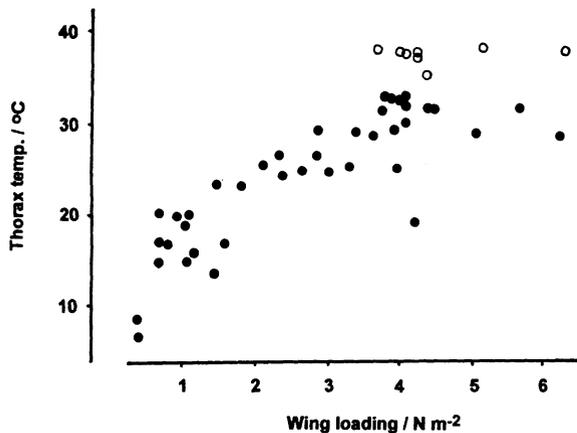


Fig. 1. Thorax temperature in flight in relation to the wing loading of earless (open circles) and tympanate (filled circles) moths from Scandinavia. Each circle represents one species (1–12 individuals per species). The earless species are of the Hepialoidea (1 species), Bombycoidea (4) and Sphingoidea (3) and the tympanate ones are of the Geometroidea (10), Drepanoidea (4) and Noctuoidea (26).

smallest species such as *Hepialus hecta* (Hepialidae; 2.1 N m^{-2}) and *Apoda limacodes* (Limacodidae; 2.4 N m^{-2}) but also in *Agria tau* (Saturniidae; 1.8 N m^{-2}), one of the largest species (Table 1). The tympanate families Notodontidae and Noctuidae differ from other tympanate families in that they generally show wing loadings as high as or higher than in some earless families.

Across all species, the wing loading was closely correlated with flight T_{th} ($r_s = 0.826$, $N = 48$, $P < 0.001$), and to a similar extent with the elevation of T_{th} above ambient ($r_s = 0.886$, $N = 48$, $P < 0.001$). The earless species on which T_{th} was measured all had wing loadings higher than 3.6 N m^{-2} (Fig. 1). Hence, the earless species had to be compared with a subset of the tympanate ones, those having wing loadings higher than 3.6 N m^{-2} . An ANCOVA showed that the T_{th} 's were significantly higher in the earless species (mean \pm S.D. was $37.3 \pm 1.0^\circ\text{C}$; $N = 8$) than in tympanate ones ($30.1 \pm 2.9^\circ\text{C}$; $N = 16$; $F = 48.6$, d.f. = 1,24, $P < 0.001$), while the effect of wing loading was barely significant ($F = 4.12$, d.f. = 1,24, $P = 0.05$). There was no significant interaction factor ($F = 0.60$, d.f. = 1,23, $P = 0.45$).

Discussion

The combination of earlessness and low wing loading (slow flight) does not seem to exist among Scandinavian "macrolepidoptera", presumably because such moths would lack appropriate defence against bats. Earless moths generally have high wing loading, which facilitates high flight speed (Norberg 1990), and they also use an elevated T_{th} in flight compared to tympanate moths. Thorax temperature is positively correlated with

flight speed and erraticism in tropical butterflies (Chai and Srygley 1990), and it seems likely that a similar situation could prevail in temperate moths. Hence, the elevated T_{th} of earless moths may be an adaptation that facilitates their flight performance and may thus explain why they tend to fly more erratically than tympanate ones (Lewis et al. 1993).

The energetic cost of warming up to a T_{th} sufficient for fast flight (Bartholomew and Casey 1978) may explain the earlier observation that earless moths show a lower tendency to resume flight after they have come to rest compared to tympanate moths (Morrill and Fullard 1991); they need more time and energy to reheat to flight temperature (Bartholomew and Heinrich 1973, Heinrich and Casey 1973, Casey and Joos 1983). Because the warming-up process is energetically costly (Bartholomew and Casey 1978) and could potentially attract the attention of gleaning bats (Faure and Barclay 1992), remaining torpid may be the best option for these moths in some situations.

Wing loading is size dependent (Norberg 1990). However, we used absolute instead of relative wing loading because it is a better predictor of absolute flight speed (Norberg 1990; U. M. Norberg pers. comm.). For protection against bats, absolute flight speed is presumably what counts, not flight speed in relation to size. Nevertheless, it is possible that large size in itself could function as defence against bats, e.g. in some Sphingidae and Saturniidae (Roeder 1974), and, if so, this could be an alternative explanation as to why some earless moths are so large. It may be relevant that the lowest wing loading among the earless moths was found in the Saturniidae, a family that typically consists of very large species (Janzen 1984).

The relationship between wing loading and presence or absence of tympanic organs is not a simple dichotomy, an observation that is not unexpected. The relatively high wing loadings of some tympanate moths, particularly notodontids and noctuids, suggest that they use multiple predator defences or that fast flight and high T_{th} 's also have other important functions in moths (Svensson 1996, Heinrich 1977). However, it should be noticed that the Notodontidae, which have the highest mean wing loading among the tympanate families, also seem to have the simplest ears with only a single auditory neuron (Surlykke 1984) and the Noctuidae, which also generally have high wing loadings, have two auditory neurones (Roeder 1967). In contrast the Geometridae, which generally have low wing loadings, seem to have the most elaborate auditory system with four neurons (Surlykke and Filskov 1997).

The relationship between the presence or absence of ultrasonic hearing and the wing loading is probably complicated by several other factors as well. For example, tympanic organs, especially those in the Noctuoidea, occupy a considerable portion of the thorax at the expense of the flight muscles (Scoble 1992). Thus

the evolution of ears would in itself have necessitated a reduction in flight performance in these moths. However, space restriction in the thorax is probably not a general explanation for the relatively low wing loadings (and T_{th} 's) of tympanate moths because the Geometroidea, Drepanoidea and Pyraloidea, which have abdominal ears (Scoble 1992), have even lower wing loadings than most Noctuoidea.

In the fossil record the earliest convincing specimens of tympanate moth families are in Baltic amber from the late Eocene or early Oligocene (Ross and Jarzembowski 1993). The evolution of the tympanum in moths follows the appearance and early radiation of the bats in the early Eocene (Jepsen 1970); an event that presumably imposed a selective pressure favouring moths that could elude the new predators either by detecting biosonar signals and taking evasive action or by fast or erratic flight. The presence of tympanic organs and high wing loadings in moths are examples of convergent evolution, with both attributes being found among different superfamilies. Hence, bat predation seems to have exerted a profound effect on the morphology (size and wing loading) and physiology (flight body temperature) of moths, just as bird predation has on butterflies (Chai and Srygley 1990, Marden and Chai 1991).

Because the non-tympanate moths lack an early warning system, their evasive response must operate continuously while in flight, and a higher energy expenditure seems to be the price they pay for being earless. Increased energy expenditure may in turn have several ecological and evolutionary consequences, including a shortened adult life span or a need to feed regularly (Bartholomew et al. 1981, Janzen 1984). The high energy demand of the non-tympanate moths could underlie their limited evolutionary success, as reflected in their relatively low species diversity. Among other things the evolution of tympanic organs could have facilitated cold adaptation (Casey and Joos 1983, Marden 1995), because it solved the problem of efficient predator avoidance at slow flight speeds and low T_{th} (Svensson et al. 1999). Moth ears can probably be considered as "key innovations" (Heard and Hauser 1995), because they may have facilitated the radiation of relatively slow flying, tympanate moths.

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Appendix

Wing loading and thorax temperature (T_{th}) measurements of larger moths belonging to eight families and six superfamilies. Asterisks denote tympanate families. N_1 is the sample size for wing loading measurements and N_2 that for body temperature readings. T_a is ambient temperature.

Family	Species	Wing loading ($N\ m^{-2}$)	N_1	T_{th} (°C)	$T_{th} - T_a$ (°C)	N_2
HEPIALOIDEA						
Hepialidae	<i>Hepialus sylvina</i>	3.66	5	37.9	18.7	9
GEOMETROIDEA						
Geometridae*	<i>Alsophila aescularia</i>	0.43	5	8.5	1.5	1
	<i>Rheumaptera cervinalis</i>	1.12	4	14.8	7.3	1
	<i>Odontopera bidentata</i>	1.83	5	23.2	10.9	3
	<i>Crocallis elinguarua</i>	1.50	5	23.5	8.3	3
	<i>Apochemia pilosaria</i>	1.47	5	13.7	8.9	6
	<i>Biston betularia</i>	2.86	5	26.2	14.8	4
	<i>Agriopsis marginaria</i>	0.44	5	6.8	1.8	2
	<i>Alcis repandata</i>	0.70	5	16.8	6.0	4
	<i>Arichanna melanaria</i>	0.92	5	19.9	7.6	4
	<i>Campaea margaritata</i>	0.69	3	14.4	2.8	3
DREPANOIDEA						
Drepanidae*	<i>Thyatira batis</i>	2.16	4	25.5	12.7	1
	<i>Tethea or</i>	2.38	1	24.1	13.3	1
	<i>Ochropacha duplaris</i>	1.18	4	15.9	6.3	3
	<i>Achlya flavicornis</i>	4.24	5	22.9	18.8	2
BOMBYCOIDEA						
Lasiocampidae	<i>Poecilocampa populi</i>	4.12	5	37.3	28.3	1
	<i>Malacosoma castrensis</i>	4.55	5	37.0	21.0	1
	<i>Lasiocampa trifolii</i>	4.48	5	37.4	20.7	3
	<i>Dendrolimus pini</i>	4.02	5	37.6	22.4	2
SPHINGOIDEA						
Sphingidae	<i>Sphinx pinastri</i>	5.18	2	38.0	27.71	1
	<i>Amorpha populi</i>	4.34	3	34.9	22.4	4
	<i>Pergesa porcellus</i>	6.31	2	37.9	23.9	4
NOCTUOIDEA						
Notodontidae*	<i>Phalera bucephala</i>	4.12	1	32.9	21.3	1
	<i>Peridea anceps</i>	5.70	5	31.8	19.1	12
	<i>Phoesia tremula</i>	3.86	5	32.6	16.6	3
Arctiidae*	<i>Cybosia mesomella</i>	0.69	2	20.0	8.2	2
	<i>Lithosia lurideola</i>	1.08	2	20.0	5.2	2
	<i>Arctia caja</i>	3.75	1	31.4	19.7	3
	<i>Diacrisia sannio</i>	1.07	4	19.0	6.3	1
	<i>Spilosoma lubricipeda</i>	3.93	3	29.3	19.3	1
Noctuidae*	<i>Hypena proboscidalis</i>	0.81	5	16.3	3.7	3
	<i>Lygephila pastinum</i>	1.57	2	16.8	5.1	5
	<i>Plusia chrysis</i>	4.02	2	32.4	21.1	1
	<i>Autographa pulchrina</i>	3.37	4	29.0	18.0	1
	<i>Acronicta auricoma</i>	2.85	1	29.5	14.8	1
	<i>Rusina ferruginea</i>	2.71	5	24.7	12.5	3
	<i>Apamea lateritia</i>	4.14	5	30.0	19.6	6
	<i>Hada proxima</i>	4.40	3	31.7	20.9	1
	<i>Lacanobia thalassina</i>	3.59	5	28.6	18.2	5

Appendix (Continued)

Family	Species	Wing loading (N m ⁻²)	N_1	T_{th} (°C)	$T_{th} - T_a$ (°C)	N_2
	<i>Cerapteryx graminis</i>	3.78	1	32.8	18.6	2
	<i>Orthosia gothica</i>	3.98	5	25.0	17.3	3
	<i>Mythimna ferrago</i>	4.14	2	32.0	21.2	1
	<i>Agrotis exclamationis</i>	4.44	5	31.3	19.8	8
	<i>Ochropleura plecta</i>	3.29	4	25.2	12.3	3
	<i>Noctua pronuba</i>	5.06	5	28.9	14.9	2
	<i>Diarsia mendica</i>	2.34	5	26.3	14.0	4
	<i>Anaplectoides prasina</i>	3.02	1	26.4	14.6	1
	<i>Eurois occulta</i>	6.23	1	28.5	16.9	1