

Anti-bat flight activity in sound-producing versus silent moths

John M. Ratcliffe, Amanda R. Soutar, Katherine E. Muma, Cassandra Guignon, and James H. Fullard

Abstract: The ultrasonic clicks produced by some tiger moths — all of which possess bat-detecting ears — are effective acoustic aposematic or mimetic signals, conferring protection against aerial hawking bats. Clicks are produced in response to bat echolocation calls. Palatable, silent non-tiger-moth species with bat-detecting ears fly away from distant bats and effect erratic flight maneuvers or stop flying in response to the calls of bats nearby. These flight responses are also an effective defense. We tested the hypotheses that sound-producing tiger moths (*i*) do not exhibit the reduction in flight time typical of silent, palatable moth species when presented with ultrasound simulating bat echolocation calls and (*ii*) exhibit more flight activity than silent, palatable species both in the presence and absence of ultrasound. We found that sound-producing tiger moths did not significantly reduce flight activity to bat-like sounds and that silent tiger moths and other noctuid species did. We also found that sound-producing tiger moths flew significantly more than did silent species in both the presence and the absence of ultrasound. The benefits of acoustic aposematism may allow sound producers to spend more time aloft than silent species and thereby improve their chances of successful reproduction.

Résumé : Les clics ultrasoniques produits par certains papillons de nuit arctiidés — qui possèdent tous des organes auditifs capables de détecter les chauves-souris — sont des signaux acoustiques aposématiqués ou mimétiques efficaces, leur procurant une protection contre les chauves-souris qui chassent au vol. Les clics sont produits en réponse aux appels d'écholocation des chauves-souris. Les espèces de papillons de nuit qui ne sont pas des arctiidés, qui sont comestibles et silencieuses, mais qui possèdent des organes auditifs capables de détecter les chauves-souris, fuient les chauves-souris éloignées en vol et entreprennent des manœuvres de vol erratiques ou s'arrêtent de voler en réaction aux appels de chauves-souris rapprochées. Nous avons testé les hypothèses selon lesquelles les arctiidés qui produisent des sons (*i*) ne réduisent pas leur temps de vol comme le font typiquement les espèces de papillons de nuit comestibles et silencieuses lorsqu'on les met en présence d'appels ultrasoniques qui simulent l'écholocation des chauves-souris et (*ii*) ils ont une activité de vol plus importante que les espèces silencieuses et comestibles, tant en présence qu'en l'absence des ultrasons. Nous observons que les papillons de nuit arctiidés producteurs de sons ne réduisent pas significativement leur activité de vol en présence de sons qui imitent les chauves-souris, alors que les arctiidés silencieux et les autres espèces de noctuoides le font. Nous trouvons aussi que les arctiidés producteurs de sons volent significativement plus que ne le font les espèces silencieuses, tant en présence qu'en l'absence d'ultrasons. Les bénéfices de l'aposématisme acoustique peuvent permettre aux producteurs de sons de passer plus de temps en vol que les espèces silencieuses et ainsi améliorer leurs chances de réussir leur reproduction.

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Introduction

For moths with bat-detecting ears, anti-bat flight behaviours are characterized by (*i*) negative phonotaxis in responses to the calls of distant bats and (*ii*) by sudden or erratic evasive flight and flight cessation in response to the intense echolocation calls of bats nearby (Roeder 1967,

1974; Miller and Surlykke 2001). Both ears and the flight behaviours they initiate appear to have evolved in moths as a defense against echolocating bats (Fullard 1988; Conner 1999; Fullard et al. 2007). These strategies confer considerable benefits to moths. Palatable moths able to effect acoustically mediated evasive flight maneuvers are >40% more likely to survive a bat attack than are palatable moths not

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Table 1. Classification of the moth species used in this study based on phylogeny, tymbal structure, chemical defense, and palatability.

Family	Subfamily	Species	Tymbals ^a	Chemical defense ^b	Palatability (%) ^c
Arctiidae	Ctenuchinae	<i>Ctenucha virginica</i> (Esper, 1794)	Complex	IG, PA	<50*
Arctiidae	Arctiinae	<i>Cycnia tenera</i> Hübner, 1818	Complex	CG	0 [†]
Arctiidae	Lithosiinae	<i>Hypoprepia fucosa</i> (Hübner, 1831)	Complex	PP	0 [†]
Arctiidae	Arctiinae	<i>Halysidota tessellaris</i> (Smith, 1797)	Complex	PA	6 [†]
Arctiidae	Arctiinae	<i>Lophocampa caryae</i> Harris, 1841	Simple (NF)	Unknown	100*
Noctuidae	Pantheinae	<i>Panthea furcilla</i> (Packard, 1864)	Absent	Unknown	100*
Notodontidae	Heterocampinae	<i>Schizura leptinoides</i> (Grote 1864)	Absent	Unknown	100*
Arctiidae	Arctiinae	<i>Spilosoma virginicum</i> (Fabricius, 1798)	Simple (NF)	IG, PA	73 [†]

^aSimple, unstriated (single click rather than click train); complex, striated (click trains rather than single clicks); NF, nonfunctional (silent, proto- or vestigial structure covered with scales) (taken from Fullard and Fenton 1977; J.H. Fullard, unpublished data).

^bCG, cardiac glycosides; IG, iridoid glycosides; PA, pyrrolizidine alkaloids; PP, polyphenolics (compiled from Cohen and Brower 1983; Goss 1979; Hristov and Conner 2005a; Nishida 2002; Weller et al. 1999).

^cPalatability to vespertilionid bats: *, J.M. Ratcliffe and J.H. Fullard, unpublished data; †, taken from Hristov and Conner 2005a.

so able (Roeder and Treat 1962; Roeder 1967; Dunning et al. 1992; Acharya and Fenton 1992, 1999).

Based on field observations of bat–moth interactions, Dunning (1968) and Dunning et al. (1992) suggested that sound-producing tiger moth species — defended through acoustic aposematism or acoustic mimicry — maintain normal flight in the presence of bats and therefore do not exhibit one or both of the defensive flight behaviours characteristic of silent and palatable moths. Our purpose here was to use a previously described quantitative behavioural assay (Fullard et al. 2003, 2004) to test Dunning's (1968) hypothesis that sound-producing tiger moths (whether noxious models or palatable mimics) do not exhibit the evasive flight behaviours typical of silent, palatable species with similarly sensitive bat-detecting ears under controlled conditions and over an extended period of time.

Materials and methods

Animals

Experiments were conducted at Queen's University Biological Station (QUBS) near Chaffey's Lock, Ontario, Canada (43° 34'N, 79° 15'W), between 18 June and 29 July 2003. Male moths were captured from fluorescent and mercury vapour light traps and identified to species using criteria in Ward et al. (1974), Covell (1984), and Riotte (1992). The general auditory sensitivity of all species used in the present study to the peak frequencies of sympatric echolocating bats is similar (Fullard and Barclay 1980; Fullard and Dawson 1999; J.H. Fullard, unpublished data). All are active at night (Fullard and Napoleone 2001; J.H. Fullard, unpublished data) and thus potential prey for the eight species of insectivorous vespertilionid bats found at and around QUBS (five residential, three migratory). Six species were selected from the family Arctiidae (= Noctuidae: Arctiinae; Lafontaine and Fibiger 2006), and one each from the families Noctuidae and Notodontidae (Table 1). A priori power analysis of the paired sample one-tailed *t* tests producing significant results reported in Fullard et al. (2003) indicated that sample sizes of five or six individuals per species produced an estimated power of 0.82 or 0.89, respectively (for details see Fullard et al. 2004). For all species (see Table 1), save *Ctenucha virginica*, we used 6 individuals; for *C. virginica* we used 5 individuals. One-tailed tests and a priori power analyses are appropriate given the first hypothesis

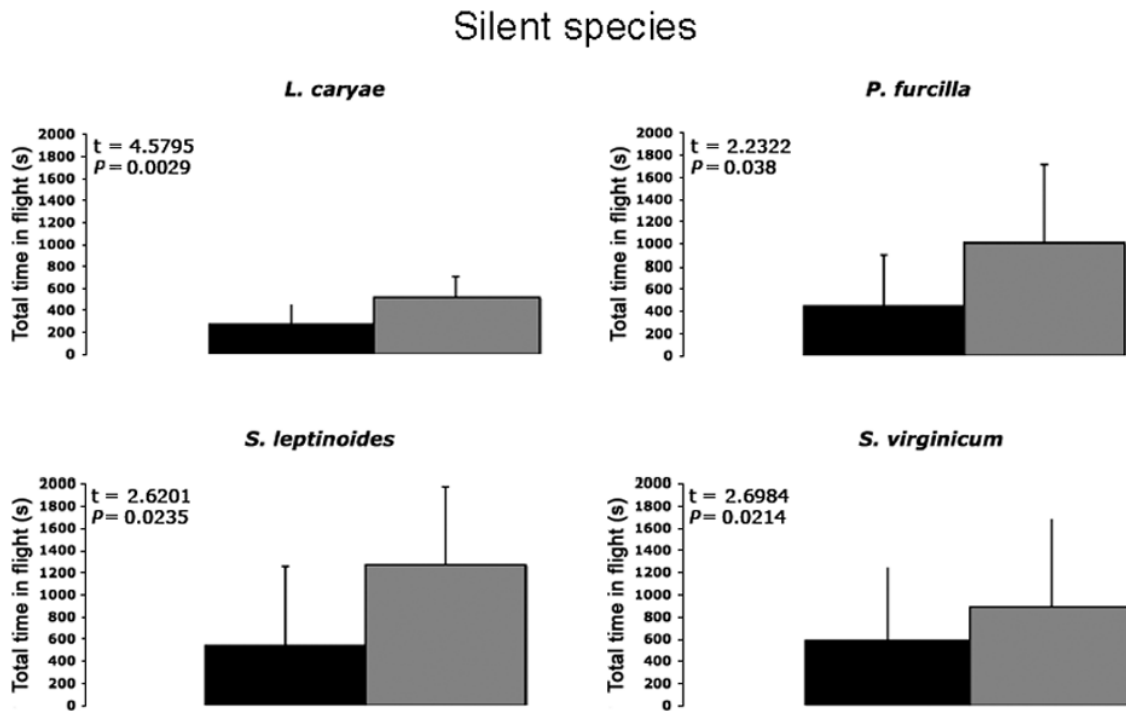
being tested (i.e., that sound-producing tiger moths exhibit reduced flight cessation relative to silent species rather than simply differ in response to bat-like sounds from silent species). When there was no a priori reason to use a one-tailed test, two-tailed tests were employed.

Experimental design

The method for quantifying the moth flight acoustic startle response of Fullard et al. (2003, 2004) was used in this study and is briefly described here. Each night, within a screen tent positioned in partially open, mixed deciduous forest, three moths of three different species were placed in individual, visually isolated screen chambers (half cylinders, 15.2 cm high × 6.5 cm radius) and videotaped for 6 h with a near-infrared camera between 2200 and 0400 (for a discussion of the validity of using cylinders to measure flight refer to Fullard and Napoleone 2001 and Soutar and Fullard 2004). Moths were exposed to simulated sympatric bat calls (based on those described for the big brown bat, *Eptesicus fuscus* (Beauvois, 1796), by Surlykke and Moss 2000) consisting of 25 kHz, 10 ms synthesized tones amplified to 94 dB peSPL (relative to a continual tone at 25 kHz; intensity of *E. fuscus* calls for prey 1 m from bat; Kick and Simmons 1984) and broadcast at a rate of 12.5·s⁻¹ from a speaker mounted 60 cm from the moths to ensure an equal intensity sound field. Sounds of this frequency, intensity, and duty cycle induce the flight reduction in silent eared moths sympatric with bats and elicit clicks in the sound-producing species tested here (Fullard 1979; Fullard and Fenton 1977; Fullard et al. 2003).

Nightly observation periods were randomly divided into thirty-six 10 min bins of which half were designated “sound” and half “no-sound”. During sound bins, pulses were delivered to the moths for 1 min followed by 1 min of silence. During no-sound bins, moths were exposed to the same playback equipment (and attendant electronic noise) as during sound bins but without the synthetic bat pulses. Moths were deemed to be “in-flight” if they were observed moving about their cage while they were flapping their wings and “not flying” if stationary. We therefore classified both actual flight and wing fluttering accompanied by walking as “in-flight”. Total flight time within each sound bin was recorded. For further details refer to Fullard and Napoleone (2001) and Fullard et al. (2003, 2004). Flight times

Fig. 1. Flight responses of silent noctuid moths *Lophocampa caryae*, *Panthea furcilla*, *Schizura leptinoides*, and *Spilosoma virginicum*. Total flight times are expressed as means + 1 SD when randomly exposed to 3 h of simulated bat calls (sound; solid bars) and 3 h of silence (no sound; shaded bars).



were scored blind to the moths' species identification, sound or no-sound bins, and acoustic class (sound-producing species or silent species).

Results

Over a 6 h period, we compared flight activity in the presence of bat echolocation calls between sound-producing arctiid species and silent arctiid, noctuid, and notodontid species. These three groups of taxa belong to the superfamily Noctuoidea (Mitchell et al. 2000; Lafontaine and Fibiger 2006). Silent and palatable noctuid moths characteristically exhibit (i) negative phonotaxis to the echolocation calls of distant bats and (ii) flight cessation when confronted by the relative louder calls of bats nearby (Roeder 1962; Fullard et al. 2003, 2004). The second class of anti-bat flight behaviour will result in an observed reduction in flight time within the confines of the screened cages used in this study; the first class may or may not. We found that all four silent moth species tested flew significantly less when exposed to ultrasound (one-tailed paired t tests for means; Fig. 1). None of the four sound-producing tiger moths exhibited a significant reduction in flight time (one-tailed t tests for means; Fig. 2). When pooled, silent species showed a significantly greater percent reduction in flight time (i.e., $1 - (\text{mean species' total flight time during ultrasound} / \text{mean species' total flight time during silent periods})$) relative to sound-producing species (two-tailed two-sample t test assuming unequal variances; $N = 8$, $t = 3.7367$, $P = 0.0134$). Overall, sound-producing species flew significantly more when exposed to either ultrasound or silence than did silent species (two-tailed two-sample t tests as-

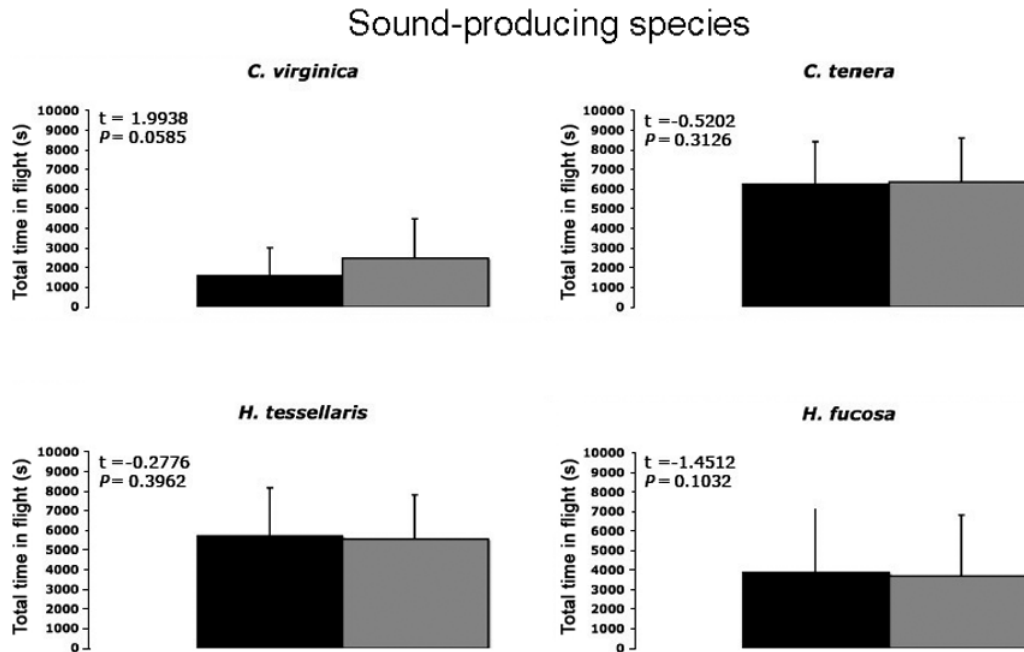
suming unequal variances; ultrasound: $N = 8$, $t = 3.6731$, $P = 0.0349$; silence: $N = 8$, $t = 4.0167$, $P = 0.0277$).

Discussion

The results of our experiment support Dunning's (1968) hypothesis that bat echolocation calls evoke less defensive flight behaviour in sound-producing tiger moths than these acoustic predator cues elicit in silent tiger moths and other species belonging to the eared moth superfamily Noctuoidea (Figs. 1, 2). When exposed to ultrasound, all four silent species significantly reduced their time in flight. Under the same conditions, the four sound-producing species did not significantly reduce their time in flight. Sound-producing tiger moths thus appear to have lost or reduced some or all of the anti-bat defensive flight behaviours typical of silent eared species living sympatrically with insectivorous bats (Fullard et al. 2003, 2004). Our results also show that sound-producing tiger moths fly more often, regardless of the presence of echolocating bats, than do silent moth species with similarly sensitive ears.

Our results and those of Dunning (1968) and Dunning et al. (1992) do not agree with those of Agee (1969), Roeder (1974), and Fullard (1979), all of whom found that sound-producing tiger moths suspended on a wire tether flapped their wings erratically and (or) ceased flight activity when played simulated bat echolocation calls. However, none of these studies measured evasive responses for longer than a few seconds. There are at least three plausible explanations for this discrepancy. First, overextended exposure to bat sounds (within 10 min sound bins and (or) over the entire 6 h period) may result in sound-producing tiger moths

Fig. 2. Flight responses of sound-producing arctiid moths *Ctenucha virginica*, *Cycnia tenera*, *Halysidota tessellaris*, and *Hypoprepia fucosa*. Total flight time are expressed as means + 1 SD when randomly exposed to 3 h of simulated bat calls (sound; solid bars) and 3 h of silence (no sound; shaded bars). Note the difference in maximum y-axis values between Figs. 1 and 2.



quickly habituating to these predator cues and recommencing flight more readily than silent species; however, the coarse scale measure of flight behaviour used in our study for both within and between sound bins does not allow for adequate assessment of this possibility. Second, sound-producing tiger moths may still exhibit moth typical near-bat defensive flight behaviours, but do so only in response to bats closer to the moths' ears than is typical of silent species or to bats using call emission patterns indicative of a bat in the last stages of attack (e.g., the terminal buzz rather than the approach phase) (J.R. Barber, personal communication). If this were the case, it would suggest that negative phonotaxis does not result in flight cessation in our behavioural assay or that sound-producing tiger moths have lost this first line of defence (as suggested by the results of Dunning et al. 1992). Third, taken together with the results of Dunning's "real world" experiments, the results from our quantitative assay should be considered a better predictor of what sound-producing tiger moths do in nature rather than what these same animals have been observed to do under tethered, laboratory conditions and short-term exposure to simulated predator cues.

The costs of anti-bat flight behaviours include reduced flight time, greater energy expenditure, and loss of female pheromone plumes (Acharya and McNeil 1998; Skals et al. 2005). Evasive or erratic flight in Lepidoptera is energetically expensive (Srygley and Chai 1990; Marden and Chai 1991), in eared moths more often than not terminating when the individual dives to ground or water (Roeder 1962, 1964; Roeder and Treat 1961, 1962), behaviour that puts the moth at risk from terrestrial and aquatic predators (Packard 1904; Guignion and Fullard 2004). Furthermore, male moths presumably lose valuable time and energy that are better spent finding and (or) following pheromone plumes to sexu-

ally receptive females as a result of the echolocation calls of bats eliciting defensive flight behaviours (Acharya and McNeil 1998; Skals et al. 2005). Time and energy are especially important considerations for understanding the evolutionary ecology of defense in moths: for most species, the adult insect is a short-lived vehicle for reproduction, having lost many of the structures required for food consumption and digestion during metamorphosis (Grzimek 1968).

In naïve red bats, *Lasiurus borealis* (Müller, 1776), clicking, sound-producing tiger moths deterred ~80% of aerial hawking attacks after several trials (Hristov and Conner 2005b; Barber and Conner 2007). In wild-caught adult northern long-eared bats, *Myotis septentrionalis* (Trouessart, 1897), clicks deterred ~70% of attacks on toxic tiger moths; of the remaining moths that were attacked, ~75% survived (protected presumably by endogenous chemical cues) (Ratcliffe and Fullard 2005). The pursuit-detering effect that these sounds have against both naïve and experienced bats suggests that even without evasive flight behaviour clicking tiger moths are better defended against aerial hawking bat attacks than are palatable and silent eared species both within the Arctiidae (= Arctiinae) and other families of eared moths.

Conclusion

Our study shows, first, that sound-producing tiger moths may have capitalized, over evolutionary time, on the protection conferred through ultrasonic sound-production against echolocating bats by reducing or losing their anti-bat flight behaviours and, second, that sound-producing species spend more time in flight in both the presence and absence of acoustic predator cues (i.e., echolocation calls) than do silent species. As a result, sound-producing tiger moths should benefit with respect to pheromone plume tracking and mate

finding success relative to silent species. Such benefits have already been proposed with respect to the greater flight activity of eared, silent and palatable species compared with the flight activity of earless moth species (Yack 1988; Soutar and Fullard 2004) where earless species have been proposed to limit nocturnal flight time as a passive defense against predation from bats (Morrill and Fullard 1992). Corroboratively, some species of visually aposematic neotropical butterflies and tiger moths do not exhibit the evasive flight behaviours typical of palatable, cryptic butterflies in response to the attacks of aerial hawking insectivorous birds (Srygley and Chai 1990; Marden and Chai 1991).

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References

- Acharya, L., and Fenton, M.B. 1992. Echolocation behaviour of vespertilionid bats (*Lasiurus cinereus* and *L. borealis*) attacking airborne targets including arctiid moths. *Can. J. Zool.* **70**: 1292–1298. doi:10.1139/z92-180.
- Acharya, L., and Fenton, M.B. 1999. Bat attacks and moth defensive behaviour around street lights. *Can. J. Zool.* **77**: 27–33. doi:10.1139/cjz-77-1-27.
- Acharya, L., and McNeil, J.N. 1998. Predation risk and mating behavior: the responses of moths to bat-like ultrasound. *Behav. Ecol.* **9**: 552–558. doi:10.1093/beheco/9.6.552.
- Agee, H.R. 1969. Response of flying bollworm moths and other tympanate moths to pulsed ultrasound. *Ann. Entomol. Soc. Am.* **62**: 801–807.
- Barber, J.R., and Conner, W.E. 2007. Acoustic mimicry in a predator-prey interaction. *Proc. Natl. Acad. Sci. U.S.A.* **104**: 9331–9334. doi:10.1073/pnas.0703627104. PMID:17517637.
- Cohen, J.A., and Brower, L.P. 1983. Cardenolide sequestration by the dogbane tiger moth. *J. Chem. Ecol.* **9**: 521–531. doi:10.1007/BF00990224.
- Conner, W.E. 1999. 'Un chant d'appel amoureux': acoustic communication in moths. *J. Exp. Biol.* **202**: 1711–1723. PMID:10359675.
- Covell, C.V., Jr. 1984. A field guide to the moths of eastern North America. Houghton Mifflin, New York.
- Dunning, D.C. 1968. Warning sounds of moths. *Z. Tierpsychol.* **25**: 129–138. PMID:5693332.
- Dunning, D.C., Acharya, L., Merriman, C.B., and Ferro, L.D. 1992. Interactions between bats and arctiid moths. *Can. J. Zool.* **70**: 2218–2223. doi:10.1139/z92-298.
- Fullard, J.H. 1979. Behavioral analyses of auditory sensitivity in *Cygnia tenera* (Lepidoptera: Arctiidae). *J. Comp. Physiol.* **129**: 79–83. doi:10.1007/BF00679914.
- Fullard, J.H. 1988. The tuning of moth ears. *Experientia* (Basel), **44**: 423–428.
- Fullard, J.H., and Barclay, R.M.R. 1980. Audition in spring species of arctiid moths as a possible response to differential levels of insectivorous bat predation. *Can. J. Zool.* **58**: 1745–1750. doi:10.1139/z80-241.
- Fullard, J.H., and Dawson, J.W. 1999. Why do diurnal moths have ears? *Naturwissenschaften*, **86**: 276–279. doi:10.1007/s001140050613.
- Fullard, J.H., and Fenton, M.B. 1977. Acoustic and behavioural analyses of the sounds produced by some species of Nearctic Arctiidae (Lepidoptera). *Can. J. Zool.* **55**: 1213–1224. doi:10.1139/z03-019.
- Fullard, J.H., and Napoleone, N. 2001. Diel flight periodicity and the evolution of auditory defences in the Macrolepidoptera. *Anim. Behav.* **62**: 349–368. doi:10.1006/anbe.2001.1753.
- Fullard, J.H., Muma, K.E., and Dawson, J.W. 2003. Quantifying an anti-bat flight response in eared moths. *Can. J. Zool.* **81**: 395–399. doi:10.1139/z03-019.
- Fullard, J.H., Ratcliffe, J.M., and Soutar, A.R. 2004. Extinction of the acoustic startle response in moths endemic to a bat-free habitat. *J. Evol. Biol.* **17**: 856–861. doi:10.1111/j.1420-9101.2004.00722.x. PMID:15271085.
- Fullard, J.H., Ratcliffe, J.M., and ter Hofstede, H. 2007. Neural evolution in the bat-free habitat of Tahiti: partial regression in an anti-predator auditory system. *Biol. Lett.* **3**: 26–28. doi:10.1098/rsbl.2006.0550. PMID:17443957.
- Goss, G.J. 1979. The interaction between moths and plants containing pyrrolizidine alkaloids. *Environ. Entomol.* **8**: 487–493.
- Grzimek, B. 1968. Grzimek's animal life encyclopedia. Vol. 2. Van Nostrand Reinhold, New York.
- Guignon, C., and Fullard, J.H. 2004. A potential cost of responding to bats for moths flying over water. *Can. J. Zool.* **82**: 529–532. doi:10.1139/z04-015.
- Hristov, N.I., and Conner, W.E. 2005a. Effectiveness of tiger moth (Lepidoptera, Arctiidae) chemical defenses against an insectivorous bat (*Eptesicus fuscus*). *Chemoecology*, **15**: 105–113. doi:10.1007/s00049-005-0301-0.
- Hristov, N.I., and Conner, W.E. 2005b. Sound strategy: acoustic aposematism in the bat-moth arms race. *Naturwissenschaften*, **92**: 164–169. doi:10.1007/s00114-005-0611-7. PMID:15772807.
- Kick, S.A., and Simmons, J.A. 1984. Automatic gain control in the bat's sonar receiver and the neuroethology of echolocation. *J. Neurosci.* **4**: 2725–2737. PMID:6502201.
- Lafontaine, J.D., and Fibiger, M. 2006. Revised higher classification of the Noctuoidea (Lepidoptera). *Can. Entomol.* **138**: 610–635.
- Marden, J.H., and Chai, P. 1991. Aerial predation and butterfly design: how palatability, mimicry, and the need for evasive flight constrain mass allocation. *Am. Nat.* **138**: 15–36. doi:10.1086/285202.
- Miller, L.A., and Surlykke, A. 2001. How some insects detect and avoid being eaten by bats: the tactics and counter tactics of prey and predator. *Bioscience*, **51**: 570–581. doi:10.1641/0006-3568(2001)051[0570:HSIDAA]2.0.CO;2.
- Mitchell, A., Mitter, C., and Regier, J.C. 2000. More taxa or more characters revisited: combining data from nuclear protein-encoding genes for phylogenetic analyses of Noctuoidea (Insecta: Lepidoptera). *Syst. Biol.* **49**: 202–224. doi:10.1080/10635159950173816. PMID:12118405.
- Morrill, S.B., and Fullard, J.H. 1992. Auditory influences on the flight behaviour of moths in a Nearctic site. I. Flight tendency. *Can. J. Zool.* **70**: 1097–1101. doi:10.1139/z92-153.
- Nishida, R. 2002. Sequestration of defensive substances from plants by Lepidoptera. *Annu. Rev. Entomol.* **47**: 57–92. doi:10.1146/annurev.ento.47.091201.145121. PMID:11729069.

- Packard, A.S. 1904. The origin of the markings of organisms (Poe-cilogenesis) due to the physical rather than to the biological environment, with criticisms of the Bates-Muller hypotheses. *Proc. Am. Philos. Soc.* **43**: 393–450.
- Ratcliffe, J.M., and Fullard, J.H. 2005. The adaptive function of tiger moth clicks against echolocating bats: an experimental and synthetic approach. *J. Exp. Biol.* **208**: 4689–4698. doi:10.1242/jeb.01927. PMID:16326950.
- Riotte, J.C.E. 1992. Annotated list of Ontario Lepidoptera. *R. Ont. Mus. Life Sci. Misc. Publ.*
- Roeder, K.D. 1962. The behaviour of free flying moths in the presence of artificial ultrasonic pulses. *Anim. Behav.* **10**: 300–304. doi:10.1016/0003-3472(62)90053-2.
- Roeder, K.D. 1964. Aspects of the noctuid tympanic nerve response having significance in the avoidance of bats. *J. Insect Physiol.* **10**: 529–546. doi:10.1016/0022-1910(64)90025-3.
- Roeder, K.D. 1967. Nerve cells and insect behavior. Harvard University Press, Cambridge, Mass.
- Roeder, K.D. 1974. Acoustic sensory responses and possible bat evasion tactics of certain moths. *In* Proceedings of the Annual Meeting of the Canadian Society of Zoologists. *Edited by* M.B.D. Burt. University of New Brunswick Press, Fredericton. pp. 71–78.
- Roeder, K.D., and Treat, A.E. 1961. The detection and evasive of bats by moths. *Am. Sci.* **49**: 135–148.
- Roeder, K.D., and Treat, A.E. 1962. The acoustic detection of bats by moths. *In* Proceedings of the 11th International Congress of Entomology, Vienna, Austria, 1960. Vol. 3. *Edited by* H. Strouhal and M. Beier. Naturhistorisches Museum, Wien, Austria. pp. 7–11.
- Skals, N., Anderson, P., Kannevorff, M., Löfstedt, C., and Surlykke, A. 2005. Her odours make him deaf: crossmodal modulation of olfaction and hearing in a male moth. *J. Exp. Biol.* **208**: 595–601. doi:10.1242/jeb.01400. PMID:15695752.
- Soutar, A., and Fullard, J.H. 2004. Nocturnal anti-predator adaptations in eared and earless Nearctic Lepidoptera. *Behav. Ecol.* **15**: 1016–1022. doi:10.1093/beheco/arh103.
- Srygley, R.B., and Chai, P. 1990. Flight morphology of Neotropical butterflies: palatability and distribution of mass to the thorax and abdomen. *Oecologia (Berl.)*, **84**: 491–499.
- Surlykke, A., and Moss, C.F. 2000. Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and laboratory. *J. Acoust. Soc. Am.* **108**: 2419–2429. doi:10.1121/1.1315295. PMID:11108382.
- Ward, P.S., Harmsen, R., and Hebert, P.D.N. 1974. The Macroheterocera of south-eastern Ontario. *J. Res. Lepid.* **13**: 23–42.
- Weller, S.J., Jacobson, N.L., and Connor, W.E. 1999. The evolution of chemical defenses and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biol. J. Linn. Soc.* **68**: 557–578.
- Yack, J.E. 1988. Seasonal partitioning of atympanate moths in relation to bat activity. *Can. J. Zool.* **66**: 753–755. doi:10.1139/z88-111.