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Ultrasonic Signals in the Defense and Courtship of *Euchaetes egle* Drury and *E. bolteri* Stretch (Lepidoptera: Arctiidae)

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Euchaetes egle *Drury and* E. bolteri *Stretch produce ultrasound using paired thoracic tymbal organs in both defensive and sexual contexts. The defensive ultrasound produced in response to tactile stimulation is fully characterized. The sounds are sexually monomorphic and species specific in the number of sound pulses produced during each flexion and relaxation of the tymbal, peak frequency, peak intensity, and duration of the interval between flexion and relaxation. Ultrasonic signals play a role in the courtship of both species. Males produce ultrasound just prior to contact with females, and it is shown to be important to courtship success in* E. egle. *Ultrasonic courtship communication is mapped on a recently proposed cladogram for the family Arctiidae. The use of ultrasound in courtship has evolved on at least three occasions within the family.*

KEY WORDS: acoustic communication; Arctiidae; courtship behavior; ultrasound.

INTRODUCTION

Moths in the family Arctiidae use a variety of communication cues in the moments before mating. In some species the courtship is simple and apparently involves only the release of a female sex pheromone and the attraction of a male. In others, such as *Utetheisa ornatrix*, a chemical conversation takes place, with the female initiating the conversation and the male replying with a courtship pheromone released from scent-disseminating structures called coremata (Conner *et al.*, 1981). The chemical conversation is reversed in *Creatonotos*, in

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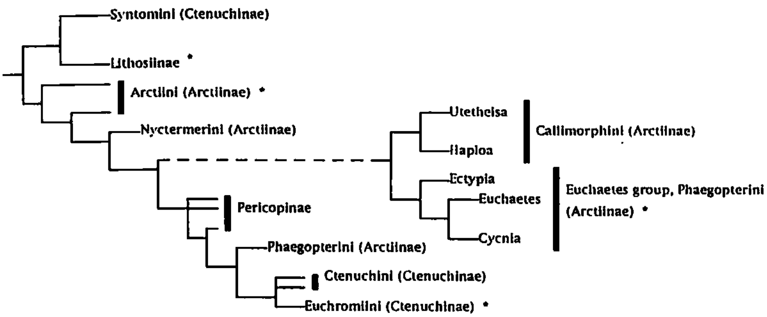

Fig. 1. A cladogram of the Arctiidae based on larval and adult morphological characteristics (Jacobson, 1994). *Demonstrated use of ultrasound in courtship.

which "lekking" males initiate courtship by releasing from spectacular abdominal coremata pheromones that attract females and other males (Wunderer *et al.*, 1986). In still other arctiids the chemical cues have been joined or supplanted by high-frequency acoustic cues. *Cycnia tenera* males simultaneously produce functionally redundant chemical and acoustic signals when they arrive at a female (Conner, 1987). *Pyrrharctia isabella* and *Phragmatobia fuliginosa* females produce sound in response to the release of a courtship pheromone by the male (Krasnoff and Yager, 1988; Krasnoff and Roelofs, 1990). Both sexes of *Empyreuma pugione* appear to use sound in courtship (Coro *et al.*, 1983; Otazo *et al.*, 1987; Portilla *et al.*, 1987; Perez *et al.*, 1988). In *Syntomeida epilais* sound production by both sexes is required for mating success, and localization of the female by the male is mediated solely by acoustic cues (Sanderford and Conner, 1990, 1995). We characterize here the acoustic signals used by two *Euchaetes* species in a defensive context and show that ultrasound production is important to courtship success in *E. egle*.

Until recently it has been difficult to place these diverse arctiid mating systems into an evolutionary context because the phylogenetic relationships of the family were largely unknown (Krasnoff and Roelofs, 1990). In 1994, however, a proposed phylogeny of the Arctiidae based on a cladistic analysis of larval and adult morphological characters was published (Jacobson, 1994). We use Jacobson's phylogeny to explore the evolution of acoustic cues in a small clade of arctiids containing the genera *Utetheisa, Haploa, Ectypia, Euchaetes,* and *Cycnia* (Fig. 1).

MATERIALS AND METHODS

Insects

Euchaetes egle were collected as larvae and adults on milkweed (*Asclepias* sp.) by Dr. James Adams in Clay County, Missouri, and by Dr. James Fullard at Queen's Biological Station, Ontario. The larvae were fed fresh leaves of *Asclepias syriaca* until pupation. *Euchaetes bolteri* larvae were collected by Dr. James Adams in Del Rio, Val Verde Co., Texas. The larvae were raised on the fresh leaves of *A. curassavica*. All larvae were held at room temperature on a 16L:8D photoperiod regime. One- to two-day-old virgin females and 1- to 7-day-old virgin males were used in the mating experiments. All behavioral observations reported here were of *Euchaetes egle* unless noted otherwise.

Tymbal Morphology

Air-dried tymbals were coated with palladium gold (Pelco SC-4 sputter coater) and viewed and photographed using an Amray 1810 scanning electron microscope. The number of microtymbals in the striated band of each tymbal was determined from SEM photographs and verified by a naive observer. Independent *t* tests were used to compare the number of microtymbals between sexes and species. Mean values are expressed throughout the text as mean ± standard deviation (sample size).

Acoustic Analysis

Moths were induced to produce ultrasound by mild tactile stimulation (gently tapping on the head or squeezing the abdomen). The sounds produced by individual *Euchaetes* were recorded using a Bruel and Kjaer 4135 $\frac{1}{4}$-in. condenser microphone, 2639T preamplifier, and 2610 measuring amplifier fed into a Racal Store 4DS recorder operating at tape speeds of 60 or 30 in./s. Recordings were slowed 16-fold and analyzed using a Kay DSP 5500 Sonagraph. Peak and rms (root mean square) intensities were measured at a distance of 5 cm laterally perpendicular to the main body axis of the moth and are expressed as decibels relative to 0.0002 dyne/cm^2.

Behavioral Observations

The mating behavior of *Euchaetes* was observed in a wind tunnel (60 × 60 × 150 cm; windspeed, 25 cm/s). Courtship sequences were observed and videotaped under deep red illumination (<5 lux) using a GBC CCD-500E videocamera and a JVC BR9000U video recorder. Ultrasound was simultaneously detected with a QMC S200 bat detector, lowered in frequency, and recorded on the audio track of the videotape.

Experimental Manipulations

Male *Euchaetes egle* were silenced by placing a drop of Elmer's glue on both tymbals. Silencing was verified by using the QMC bat detector during tactile stimulation of the moth. Sham-operated control males had glue placed on the episternites one segment anterior to the tymbal organs. Glued moths were rechecked after each courtship sequence to ensure that the tymbals were still incapable of producing sound. The mating successes of silenced, control, and unmanipulated males were compared using a chi-square test.

RESULTS

Both *Euchaetes egle* and *E. bolteri* have a pair of well-developed sound-producing structures called tymbal organs on the lateral metathorax (Fullard and Fenton, 1977; Simmons, 1995). These tiny blisters of cuticle are elaborations of metepisternites (Blest *et al.*, 1963; Fullard and Heller, 1990). The anterior edge of each tymbal, the striated band (Forbes and Franclemont, 1958), is heavily invested with ridges, or microtymbals, and largely devoid of scales or setae. *E. egle* males and females have 28.8 ± 4.6 ($n = 8$) and 28.0 ± 3.4 ($n = 10$) microtymbals per organ, respectively. There is no significant difference between the sexes in the number of microtymbals (t test; $P > 0.05$) and no obvious sexual dimorphism in the structures. *E. bolteri* have significantly fewer microtymbals ($P < 0.05$; interspecific comparison with sexes combined): 17.7 ± 1.7 ($n = 7$) for males and 16 ($n = 1$) for females.

Euchaetes generates ultrasound by buckling the upper portion of the striated band inward (flexion), producing a burst of source pulses, each from a single microtymbal (Fig. 2). The tymbal then recoils to its original shape (relaxation), producing a second burst of sound (Fullard and Heller, 1990).

E. egle and *E. bolteri* respond to tactile stimulation by producing a train of flexion and relaxation cycles called modulation cycles by Fullard and Fenton (1977). The modulation cycle repetition rate is quite variable; it reaches a maximum of 37.1 ± 21.0 cycles/s ($n = 10$) in *E. egle* and is similar in *E. bolteri.* The sounds produced by *Euchaetes* tymbals are broadband in frequency and sexually monomorphic. The characteristics of the sounds of each sex and species are summarized in Table I. *E. egle* produces a significantly greater number of sound pulses per flexion and relaxation cycle (consistent with their greater number of microtymbals) and has a significantly higher peak frequency, a slightly higher peak intensity, and a shorter time interval between flexion and relaxation. Both species can use their tymbals singly, together simultaneously, or together in an alternating fashion (Fig. 2). Under the mild tactile stimulation used in this study the moths used only one-fifth of the microtymbals during sound production (compare number of sound pulses for flexion or relaxation to the number of microtymbals for each species). This fraction may increase in different contexts or under more intense stimulation (Fullard, 1992).

Euchaetes males produce trains of ultrasonic clicks during courtship just prior to and during contact with the female. When the tymbals of male *E. egle* were immobilized with glue, no ultrasound was detected during courtship, suggesting that either males are the sole sound producers during courtship or they

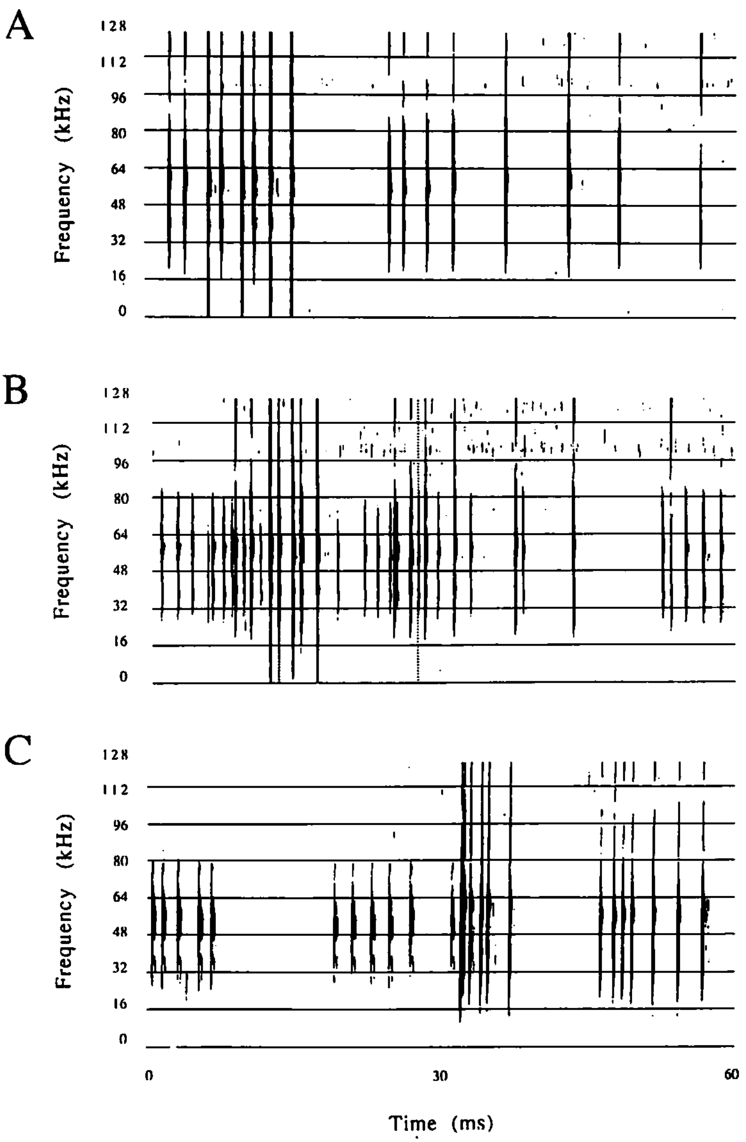

Fig. 2. Wideband sonograms (100-pt, 300-Hz filter) of the clicks produced by a male *E. egle* in response to tactile stimulation. (A) Sound production by proximal tymbal only. (B) Sound production by both tymbals simultaneously. (C) Sound production by both tymbals in an alternating fashion.

Table I. Characteristics of Ultrasound Produced by *E. egle* and *E. bolteri* in Response to Moderate Tactile Stimulation

Sex/species	Frequency range (kHz)[a]	Peak frequency (kHz)*	Pulses per flexion*	Pulses per relaxation*	Peak intensity (dB)*	rms intensity (dB)	Duration of flexion (ms)	Duration of interval (ms)*	Duration of relaxation (ms)
Male *E. egle*	39.5 ± 8.3 to 64.4 ± 3.4 (n = 10)	56.2 ± 6.3 (n = 10)	6.0 ± 2.4 (n = 10)	5.7 ± 2.7 (n = 10)	87.4 ± 8.9 (n = 12)	59.6 ± 4.0 (n = 12)	7.8 ± 4.6 (n = 10)	10.5 ± 5.2 (n = 10)	14.0 ± 4.6 (n = 10)
Female *E. egle*	30.4 ± 9.0 to 64.1 ± 5.7 (n = 10)	57.4 ± 5.8 (n = 10)	5.6 ± 2.6 (n = 10)	5.8 ± 3.1 (n = 10)	84.3 ± 8.9 (n = 12)	62.9 ± 5.9 (n = 12)	6.7 ± 5.4 (n = 10)	9.7 ± 2.5 (n = 10)	13.7 ± 6.3 (n = 10)
Male *E. bolteri*	30.3 ± 12.4 to 59.5 ± 6.8 (n = 8)	49.9 ± 9.0 (n = 8)	3.6 ± 1.1 (n = 9)	3.3 ± 1.3 (n = 9)	78.9 ± 7.2 (n = 4)	59.3 ± 2.4 (n = 4)	7.2 ± 4.0 (n = 9)	14.0 ± 5.8 (n = 9)	9.9 ± 6.7 (n = 9)
Female *E. bolteri*	10.9 to 54.4 (n = 1)	49.9 (n = 1)	3 (n = 1)	2 (n = 1)	—	—	9.3 (n = 1)	13.7 (n = 1)	16.7 (n = 1)

[a] Measured 9 dB down from the peak frequency.

*Significant interspecific difference with sexes combined (t test, $P < 0.05$).

Table II. Mating Success of *E. egle* Males with Nonfunctional (Glued) Tymbals Versus Unmanipulated and Control Males

Type of manipulation	Mating attempts	
	Number successful	Number failed
Unmanipulated (n = 9)	9	0
Glued (n = 10)	2	8
Sham-operated control (n = 6)	6	0

must initiate acoustic conversations with females. Female *E. egle* did not demonstrate any behavior (trembling, tensing, or wing fluttering) consistent with sound production, suggesting that males are the only sound producers. Males rendered incapable of sound production had reduced mating success relative to unmanipulated males and control males (Table II; $\chi^2 = 17.65$, $P < 0.001$). In most cases, unsuccessful courtships were terminated by female flight.

DISCUSSION

The metepisternal tymbal organ is a structure unique to the Arctiidae (Adams, 1990; Jacobson, 1994). Its primary function is defense against bats, where it either produces aposematic signals warning of an underlying chemical defense (Dunning, 1968; Surlykke and Miller, 1985; Dunning *et al.*, 1992) or jams the echolocation signals of bats (Fullard *et al.*, 1979; Miller, 1991). The tymbal sounds of *Euchaetes* undoubtedly evolved in this defensive context (Adams, 1990). In addition to touch, they can be elicited by bat cries and even jingling keys (Fullard and Fenton, 1977).

The characteristics of the ultrasonic clicks produced by *E. egle* and *E. bolteri* are similar to those reported by Fullard and Fenton (1977) for *E. egle*. However, the lack of sexual dimorphism in tymbal morphology and sound characteristics led Fullard (1977) to conclude that ultrasound is probably not used in arctiid mating. In contrast, we show here that ultrasound production by *Euchaetes* males plays an important role in courtship. In the absence of ultrasound, most precopulatory interactions are terminated by the female.

Based on its limited distribution within the Arctiidae, the use of ultrasound in arctiid courtship appears to have arisen secondarily. Ultrasound plays the same role in *Euchaetes* that chemical signals play in other male moths. This suggests that sound may lend an additional layer of species specificity to moth courtship (Phelan, 1992) and/or play a role in female mate choice (Conner *et al.*, 1981). The species differences shown here could result in species-specific courtship cues, and the variability in the ultrasound produced by moths could provide a substrate for mate choice. Assessment of these possibilities will require additional behavioral and comparative studies.

The small clade containing *Utetheisa, Haploa, Ectypia, Euchaetes,* and *Cycnia* contains two distinct lineages (Fig. 1). The *Utetheisa-Haploa* (Callimorphini) lineage, in which courtship is silent, is composed of species that feed for at least a portion of their larval life on plants containing pyrrolizidine alkaloids (PAs). *Utetheisa* larvae feed on the leaves, blossoms, and seeds of *Crotalaria* sp., and *Haploa* larvae feed for their first few instars on *Eupatorium* sp. before entering a larval diapause, after which they are polyphagous. Incorporated PAs have been shown to protect *Utetheisa* from invertebrate predators (Eisner and Meinwald, 1987), and PAs probably play a similar role in *Haploa*, although perhaps to a lesser degree. Males of these species rely on elaborate pheromone-disseminating structures in their courtship: genitalic coremata in *Utetheisa* (Conner *et al.*, 1981) and abdominal coremata in *Haploa* (Davidson, 1995). In each case the alkaloid-derived pheromone hydroxydanaidal has been characterized from extracts of the coremata (Conner *et al.*, 1981; Davidson, 1995). In *Utetheisa* this pheromone advertises a male's ability to provide the female with a nuptial gift of defensive alkaloids (Dussourd *et al.*, 1991).

In contrast, in species within the *Ectypia-Euchaetes-Cycnia* lineage (*Euchaetes* group), ultrasound plays a prominent role in courtship. These species feed on plants containing cardenolides, which can be used as defensive compounds and are present in *Cycnia* (Cohen and Brower, 1983). As we have shown here, however, the courtship in this lineage is very different from the courtship of *Haploa* and *Utetheisa*. Ultrasound plays a prominent role in both *Euchaetes* and *Cycnia*. *Euchaetes* and *Ectypia* (Jacobson, 1994) have no coremata, and *Cycnia* has small rudimentary coremata that are not necessary for successful courtship (Conner, 1987).

Ultrasound use in courtship has arisen at least three times in the Arctiidae: in the Arctiini in *Pyrrharctia isabella* and *Phragmatobia fuliginosa* (Krasnoff and Roelofs, 1990), in the Euchromiini in *Syntomeida epilais* (Sanderford and Conner, 1990, 1995) and *Empyreuma affinis* (Portilla *et al.*, 1987), and in the *Euchaetes* group, as described here (Fig. 1). A pattern is beginning to emerge. Arctiids that specialize for at least a portion of their larval life on plants containing PAs often use male scent-disseminating structures with a PA-derived pheromone in courtship. Arctiids that do not feed on PAs appear to favor ultrasound in their precopulatory interactions. *Pyrrharctia* and *Phragmatobia* have evolved toward polyphagy from a PA-feeding ancestor (Krasnoff and Roelofs, 1990), and the other two groups using ultrasound in courtship have shifted to cardenolide-containing plants. This correlation is logical yet puzzling. It is logical in that the PA precursors necessary for pheromone production are not available to these insects [but see Boppré (1986) for a discussion of PA sequestration in adults] but puzzling in that no arctiid is known to produce a courtship pheromone derived from a compound other than a PA. Instead when PAs are unavailable there has been a shift away from chemical communication toward ultrasound as the main short-range communication modality. For this reason future studies should concentrate on cardenolide-feeding arctiids to determine whether their use of ultrasound is common and consistent.

Future studies should also include investigations of the communicative signals in the courtship of the Lithosiinae and Pericopinae. The Lithosiinae is a basal lineage of the Arctiidae and little is known about the precopulatory interactions of this important group. Representatives feed on lichens, algae, mosses, and liverworts (Jacobsen, 1994). They are avoided by predators (Acharya and Fenton, 1992; Sargent, 1995), and their chemical defenses appear to be based on the anthraquinone paretin, the depside atranorin, and cleavage products of the latter incorporated from their food (Hesbacher *et al.*, 1995). The Pericopinae are butterfly-like in habit and some feed on plants containing cardenolides (Black, 1976). It will be important to see if their diurnal nature and feeding preferences have influenced the courtship cues that they utilize.

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NOTE ADDED IN PROOF

After preparing this manuscript we discovered the following excellent study of ultrasonic communication in the Lithosiine genus *Setina.* This brings the number of independent origins of the use of ultrasound in the courtship of the Arctiidae to four (Fig. 1).

Černý, K. (1990). Untersuchungen zur Ökophysiologie der Gattung *Setina* Schrank (Lepidoptera: Arctiidae). Ph.D. thesis, Universität in Innsbruck, Innsbruck, Austria.

REFERENCES

Acharya, L., and Fenton, M. B. (1992). Echolocation behavior of vespertillionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) attacking airborne targets including arctiid moths. *Can. J. Zool.* **70:** 1292–1298.

Adams, J. K. (1990). *The Defenses of Adult Tiger Moths (Lepidoptera: Arctiidae): Phylogenetic and Ecological Factors Influencing the Array of Defenses of Individual Species*, Ph.D. thesis, University of Kansas, Lawrence.

Black, D. W. (1976). *Studies on Cardiac Glycoside Storage in Moths*, Ph.D. thesis, University of Miami, Miami.

Blest, A. D., Collett, T. S., and Pye, J. D. (1963). The generation of ultrasonic signals by a New World arctiid moth. *Proc. Roy. Soc. Lond.* **158:** 196-207.

Boppré, M. (1986). Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaloids). *Naturwissenschaften* **73:** 17-26.

Cohen, J. A., and Brower, L. P. (1983). Cardenolide sequestration by the dogbane tiger moth (*Cycnia tenera*; Arctiidae). *J. Chem. Ecol.* **9:** 521-532.

Conner, W. E. (1987). Ultrasound: Its role in the courtship of the arctiid moth *Cycnia tenera. Experientia* **43:** 1029-1031.

Conner, W. E., Eisner, T., Vander Meer, R. K., Guerrero, A., and Meinwald, J. (1981). Precopulatory sexual interaction in an arctiid moth (*Utetheisa ornatrix*): Role of a pheromone derived from dietary alkaloids. *Behav. Evol. Sociobiol.* **9:** 227-235.

Coro, F., Perez, M., and Lopez, J. R. (1983). Emision de senales acousticas en *Empyreuma pugione* (Lepidoptera, Ctenuchidae). *Cien. Biol.* **10:** 5-18.

Davidson, R. B. (1995). *Courtship Communication in* Haploa clymene *(Brown) and* H. confusa *(Lyman) (Lepidoptera: Arctiidae: Arctiinae): Chemical Characterization of Male and Female Pheromones and Description of the Pheromone Glands*, M.S. thesis, Wake Forest University, Winston-Salem, NC.

Dunning, D. C. (1968). Warning sounds of moths. *Z. Tierpsychol.* **25:** 129-138.

Dunning, D. C., Acharya, L., Merriman, C., and Ferro, L. D. (1992). Interactions between bats and arctiid moths. *Can. J. Zool.* **70:** 2218-2223.

Dussourd, D. E., Harvis, C. A., Meinwald, J., and Eisner, T. (1991). Pheromonal advertisement of a nuptial gift by a male moth (*Utetheisa ornatrix*). *Proc. Natl. Acad. Sci. USA* **88:** 9224-9227.

Eisner, T., and Meinwald, J. (1987). Alkaloid-derived pheromones and sexual selection in Lepidoptera. In Prestwich, C. D., and Blomquist, G. J., (eds.), *Pheromone Biochemistry*, Academic Press, Orlando, FL, pp. 251-269.

Fenton, M. B., and Roeder, K. D. (1974). The microtymbals of some Arctiidae. *J. Lep. Soc.* **28:** 205-211.

Forbes, W. T., and Franclemont, J. G. (1957). The striated band (Lepidoptera, chiefly Arctiidae). *Lepidop. News* **11:** 147-150.

Fullard, J. H. (1977). Variability and absence of sexual dimorphism in sounds of *Cycnia tenera* Hubner (Lepidoptera, Arctiidae). *J. N.Y. Entomol. Soc.* **85:** 21-25.

Fullard, J. H. (1992). The neuroethology of sound production in tiger moths (Lepidoptera: Arctiidae). I. Rhythmicity and central control. *J. Comp. Physiol. A* **170:** 575-588.

Fullard, J. H., and Fenton, M. B. (1977). Acoustic and behavioral analyses of the sounds produced by some species of Nearctic Arctiidae (Lepidoptera). *Can. J. Zool.* **55:** 1213-1224.

Fullard, J. H., and Heller, B. (1990). Functional organization of the arctiid moth tymbal (Insecta, Lepidoptera). *J. Morphol.* **204:** 57-65.

Fullard, J. H., Fenton, M. B., and Simmons, J. A. (1979). Jamming bat echolocation: The clicks of arctiid moths. *Can J. Zool.* **57:** 647-649.

Hesbacher, S., Giez, I., Embacher, G., Fiedler, K., Max, W., Trawöger, A., Türk, R., Lange, O. L., and Prokosch, P. (1995). Sequestration of lichen compounds by lichen-feeding members of the Arctiidae (Lepidoptera). *J. Chem. Ecol.* **21:** 2079-2089.

Jacobson, N. L. (1994). *Cladistic Studies of the Arctiidae (Lepidoptera) and the Genus* Agylla (*Arctiidae, Lithosiinae*) *Using Characters of the Adults and Larvae*, Ph.D. dissertation, Cornell University, Ithaca, NY.

Krasnoff, S. B., and Roelofs, W. L. (1990). Evolutionary trends in the male pheromone systems of arctiid moths: Evidence from studies of courtship in *Phragmatobia fuliginosa* and *Pyrrharctia isabella* (Lepidoptera: Arctiidae). *Zoo. J. Linn. Soc.* **99:** 319-338.

Krasnoff, S. B., and Yager, D. D. (1988). Acoustic response to a pheromone cue in the arctiid moth *Pyrrharctia isabella. Physiol. Entomol.* **13:** 433-440.

Miller, L. A. (1991). Arctiid moth clicks can degrade the accuracy of range difference discrimination in echolocating big brown bats, *Eptesicus fuscus*. *J. Comp. Physiol. A* **168:** 571-579.

Otazo, A., Coro, F., and Barro, P. (1987). Papel de la olfaccion y la audicion en la conducta de apareamiento de *Empyreuma pugione* (Lepidoptera: Arctiidae). *Cien. Biol.* **17:** 41-48.

Perez, M., Portilla, N., Coro, F., and Barro, P. (1988). The auditory system of noctuid moths and its possible role in mating behavior. *Wiss Z. Humbolt-Univ. Berlin R. Math/Nat. Wiss.* **37:** 322-327.

Phelan, P. L. (1992). Evolution of sex pheromones and the role of asymmetric tracking. In Roitberg, B. D., and Isman, M. B. (eds.), *Insect Chemical Ecology*, Chapman and Hall, New York, pp. 265-314.

Portilla, N., Coro, F., Otazo, A., Perez, M., and Alonso, N. (1987). Mating behavior and auditory information flow in an arctiid moth. *Naturwissenshaften* **74:** 503-505.

Sanderford, M. V., and Conner, W. E. (1990). Courtship sounds of the polka dot wasp moth. *Naturwissenschaften* **77:** 345-347.

Sanderford, M. V., and Conner, W. E. (1995). Acoustic courtship communication in *Syntomeida epilais* Wlk. (Lepidoptera: Arctiidae, Ctenuchinae). *J. Insect Behav.* **8:** 19-31.

Sargent, T. D. (1995). On the relative acceptabilities of local butterflies and moths to local birds. *J. Lep. Soc.* **49:** 148-162.

Simmons, R. B. (1995). *Chemical and Acoustic Cues in the Courtship of* Euchaetes egle *Drury and* Euchaetes bolteri *Stretch (Lepidoptera: Arctiidae)*, M.S. thesis, Wake Forest University, Winston-Salem, NC.

Surlykke, A., and Miller, L. A. (1985). The influence of arctiid moth clicks on bat echolocation: Jamming or warning? *J. Comp. Physiol. A* **156:** 831-843.

Wunderer, H., Hansen, K., Bell, T. W., Schneider, D., and Meinwald, J. (1986). Sex pheromones of two Asian moths (*Creatonotos transiens, C. gangis*; Lepidoptera—Arctiidae): Behavior, morphology, chemistry and electrophysiology. *Exp. Biol.* **46:** 11-27.