Extinction of the acoustic startle response in moths endemic to a bat-free habitat

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Abstract

Most moths use ears solely to detect the echolocation calls of hunting, insectivorous bats and evoke evasive flight manoeuvres. This singularity of purpose predicts that this sensoribehavioural network will regress if the selective force that originally maintained it is removed. We tested this with noctuid moths from the islands of Tahiti and Moorea, sites where bats have never existed and where an earlier study demonstrated that the ears of endemic species resemble those of adventives although partially reduced in sensitivity. To determine if these moths still express the anti-bat defensive behaviour of acoustic startle response (ASR) we compared the nocturnal flight times of six endemic to six adventive species in the presence and absence of artificial bat echolocation sounds. Whereas all of the adventive species reduced their flight times when exposed to ultrasound, only one of the six endemic species did so. These differences were significant when tested using a phylogenetically based pairwise comparison and when comparing effect sizes. We conclude that the absence of bats in this habitat has caused the neural circuitry that normally controls the ASR behaviour in bat-exposed moths to become decoupled from the functionally vestigial ears of endemic Tahitian moths.

Introduction

The evolutionary changes that occur in organisms following the relaxation of selection pressure are phenomena that have received interest at the genetic and phenotypic level (Wiens, 2001; Porter & Crandall, 2003). In many cases the changes described are regressions of sensory systems [e.g. the loss of vision in cave-dwelling organisms (Jones & Culver, 1989], whereas the fate of behaviours related to those reduced traits are less understood. Understanding the integration of sensory systems and behaviours, in general, is complicated by the fact that, for most animals, behaviours are usually governed by a variety of senses and a behaviour will not necessarily be impacted by a lost sensory structure if it can be evoked by another [e.g. extraocular control of the optomotor response in blind cavefish (Teyke &

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Schaerer, 1994)]. The auditory defences of flying moths against the attacks of bats are an exception to this because most species use their ears solely to detect the echolocation calls of bats and activate evasive manoeuvres. One such behaviour is the acoustic startle response (ASR), the sudden interruption of flight in response to close bats (Roeder, 1967) and is found in a variety of night-flying insects (Hoy, 1989; Miller & Surlykke, 2001). Although some moths use sounds (and presumably ears) for social purposes, these species are phylogenetically and geographically disparate making it likely that non-bat uses for moth ears are a secondary adaptation and that bat echolocation forms the only selective influence on the ears of most moths (Roeder, 1970, 1975; Fullard, 1988; Conner, 1999; Yager, 1999). If the ears of nonacoustic moths are used only for bat detection, species that have arisen in bat-free environments should possess reduced auditory capacity and/or ASR. Although auditory reduction in some bat-released moths has been reported (Fullard *et al.*, 1997; Surlykke *et al.*, 1998), no one has demonstrated degenerative changes in the behaviours that these (or any other) regressed sensory organs govern and in a study of arctic

moths it has been suggested that the ASR has persisted in the absence of bats (Rydell *et al.*, 2000).

The high islands of French Polynesia are unique in the world in that they possess tropical habitats that have been continually bat-free since their appearance 0.25–5.78 Myr and these habitats have given rise to endemic species of moths that have evolved in the absence of this selection pressure. Fullard (1994) demonstrated that (putatively) endemic Tahitian moths possess ears that differ from those of adventives (i.e. recently arrived) only in their physiological sensitivity to high frequencies but appear otherwise normal. This finding gives rise to two possibilities: (i) the entire ASR sensoribehavioural network in these moths remains intact, or (ii) although the ears of endemics remain the behaviour they previously evoked is extinct and the ASR sensoribehavioural network has disintegrated. To test this requires a quantified measurement of the moth's flight when exposed to bat echolocation calls but reports of this behaviour have traditionally relied on qualitative observations [e.g. momentary flight reactions in free flying or tethered moths (Roeder, 1962; Roeder & Fenton, 1973; Rydell *et al.*, 2000)] that cannot be subjected to statistical analyses (but see Rydell *et al.*, 1997). Recently, Fullard *et al.* (2003) described a quantitative ASR measurement in North American moths that permits such analyses over a longer portion of the night and we have used this in our present study to test our prediction that this auditory-evoked defensive response has not been maintained by stabilizing selection in bat released, endemic Tahitian noctuid moths.

Materials and methods

Animals

We conducted our study from November 2002 to January 2003 in French Polynesia (Research Permit no. 28, Délègation Régionale à la Recherche et à la Technologie, Haut-Commissariat de Republique en Polynésie française) using the facilities of the Gump South Pacific Research Station, Moorea (University of California at Berkeley). We collected endemic moths (Family: Noctuidae) on Mount Marau (elevation: 1413 m) on the island of Tahiti and adventive moths (also Noctuidae) from two sites on the island of Moorea (Belvédère, elevation: 250 m; Gump Station, elevation: 15 m). As size appears to influence auditory sensitivity in noctuid moths (Surlykke *et al.*, 1999), the ranges of sizes of moths from both residency classes in the present study were chosen to be similar (Table 1). We identified moths according to Holloway (1983) and Orhant (2002, 2003). Moths used in the flight experiments have been deposited with Georges Orhant (Wailly-Beaucamp, France) and voucher specimens have been deposited with the Bishop Museum (Honolulu, Hawaii) and the Délègation Régionale à la

Table 1 List of the moths used in the flight trials of the current study following their taxonomic revisions (Orhant, 2002, 2003) from names used in Fullard (1994).

Species	Names in Fullard (1994)	Wing span (mm)	Sites captured	Abundance
Adventive				
Subfamily: Acronictinae				
Chasmina tibialis (Fabricus)	*Chasmina tibialis*	41–47	MO, TA	C
Leucocosmia nonagrica (Walker)	*Leucocosmia nonagrica*	29–34	MO, TA	VC
Subfamily: Catocolinae				
Mocis trifasciata (Stephens)	*Mocis trifasciata*	40–46	MO, TA	C
Achaea janata (Linné)	*Achaea janata*	46–55	MO	U
Subfamily: Acronictinae				
Aedia sericea (Butler)	*Aedia sericea*	34–39	MO	C
Subfamily: Plusiinae				
Chrysodeixis eriosoma (Doubleday)	*Chrysodeixis eriosoma*	32–38	MO, TA	VC
Endemic				
Subfamily: Herminiinae				
Hydrillodes crispipalpus Collenette	*Hydrillodes crispipalpus*	34	TA	VC
Subfamily: Amphipyrinae				
Callopistria alticola (Orhant)	*Callopistria* sp. n.1	34–38.5	TA	VC
Callopistria steevei (Orhant)	*Callopistria* sp. n.2	33–34	TA	C
Subfamily: Catocalinae				
Bastilla insularum (Orhant)	(not used in Fullard, 1994)	57–58	TA	U
Subfamily: Plusiinae				
Chrysodeixis collardi (Orhant)	*Chrysodeixis* sp. n.1	48–50	TA	U
Subfamily: Hadeninae				
Mythimna mouai (Orhant)	*Mythimna* sp.	43–49	TA	C

Each species are listed for its wing span (from M. Orhant, personal communication), the sites where it was captured (MO, Moorea; TA, Tahiti) and its relative abundance (U, uncommon; C, common; VC, very common).

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Flight measurements and auditory reanalysis

The method for quantifying the moth ASR of Fullard *et al.* (2003) was used in this study and is briefly described here. Each night, six moths of six different species were placed into individual, visually isolated screen chambers that had been washed from the trials of the previous night [see Fullard & Napoleone (2001) for discussion of the validity of using chambers for flight experiments], exposed to ambient light and temperature and videotaped for 6 h with a self-illuminated, near-infrared (wavelength 980 nm) camera (VDC 9212, Sanyo Electric Co., Ltd, Osaka, Japan). Moths were exposed to 25 kHz, 10 ms synthesized tones (Exact 126 function generator), amplified to 94 dB SPL (root mean square re 20 μPa) (LM1875T, National Semiconductor Corp. Santa Clara, CA, USA) and broadcast at a rate of 12.5 s^{-1} from a Technics EAS-10TH400B speaker mounted 60 cm from the moths to ensure an equal intensity sound field. These values were used as an approximation to the calls emitted by a typical attacking bat (*Eptesicus fuscus*) when it is 500 ms from capturing its prey (Surlykke & Moss, 2000). Nightly observation periods were randomly divided into 36 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.

The auditory sensitivity curves (audiograms) published in Fullard (1994) using putatively endemic species were reanalysed using the recent taxonomic determinations of the Tahitian moth fauna as published by Orhant (2002, 2003).

Data analyses

We analysed our results in two ways: (i) with paired sample *t*-tests using the total flight times of the adventive and endemic species when exposed to ultrasound vs. silence, and (ii) using a matched-pair comparison of the per cent change in flight times and effect sizes of the moths. Although the best way to test for lost characters would be to apply a complete phylogenetic map of noctuid species to the responses we observed (Wiens, 2001), this approach is only partially available to us due to the absence of a phylogeny for noctuid species and so we have included both methods of analysing our data. Furthermore, we believe that the incidence of ears and ASR in noctuid moths is so globally widespread (Fullard, 1998) that the loss of these traits would arise from environmental effects rather than from the accidental inclusion of pre-existing auditory states.

For our paired-sample *t*-test comparisons we estimated statistical power using results from the North American moths, *Ennomos magnaria*, *Amphipyra pyramidoides* and *Caenurgina erechtea* tested in Fullard *et al.* (2003). We conducted power analyses of paired sample, one-tailed *t*-tests using GPower (Erdfelder *et al.*, 1996). To do so, we estimated effect size for each of these North American species and used the average effect size to predetermine sample size. Power analysis indicated that a total sample size of five individuals from a species was sufficient to ensure power >0.8 ($\beta < 0.2$) at $\alpha = 0.05$ (actual power = 0.82). Six individuals produced an estimated power of 0.89 and was therefore the sample size chosen for the study reported herein.

We used the proposed phylogeny of noctuid subfamilies (Speidel *et al.*, 1996) to choose endemic vs. adventive species for matched-pair comparisons. Although only one species pair in this analysis is congeneric, the other pairs were chosen to minimize phylogenetic distance according to Speidel *et al.* (1996). In the case of two species within a single subfamily, the species pair was determined by a coin toss. The mean per cent differences in flight times when exposed to ultrasound and the paired-sample effect size (Horton, 1995) were compared using paired-sample *t*-tests. All results were compared using one-tailed tests, as it was assumed that moths only reduce their flight under these acoustic stimuli (Fullard *et al.*, 2003).

Results

Animals

Table 1 lists the moths that were used in the auditory experiments of Fullard (1994) and the flight trials of the current study along with their residency status, size, relative abundance and revised taxonomic status as described in Orhant (2002, 2003). Although adventive species occur in sites on both islands, endemics are only found at the high altitude locations of the island of Tahiti although many are common in these sites.

Flight measurements and auditory reanalysis

There were no differences between the no-sound flight time of males and females in any of the species used (General Linear Model ANOVA: $F_{1,10} = 0.404$, n.s.) so flight times for all species were pooled. Figure 1a illustrates the ASR to pulsed ultrasound in the two residency classes of moths. Noctuid moths characteristically exhibit erratic flight and/or cease flying when confronted by loud (i.e. near) bats (Roeder, 1962; Rydell *et al.*, 1997) and whereas all six adventive species of moths flew significantly less when exposed to ultrasound, only one of the six endemic species exhibited a significant reduction in flight time.
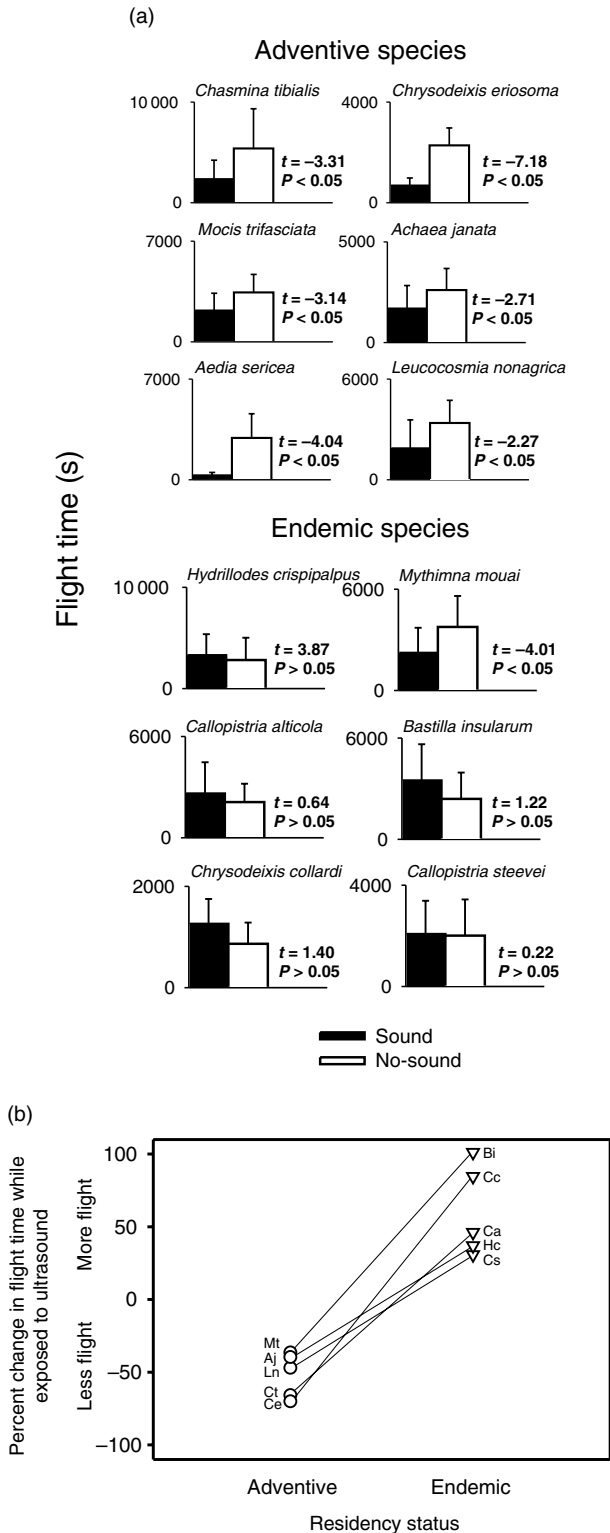
(a)

Fig. 1 Flight responses of adventive and endemic moths. (a) Total flight times expressed as mean (+1 SD) of moths (for all species except *Hydrillodes crispipalpus*, $n = 6$, *H. crispipalpus*, $n = 5$) when randomly exposed to 3 h of simulated bat calls (Sound) and 3 h of silence (No-sound). Statistics reported refer to one-tailed probability of no-sound flight time exceeding sound flight time, *P*-value for *H. crispipalpus* based upon this expected difference. (b) Results of the matched-pair comparison of related species chosen from the phylogeny of Speidel *et al.* (1996), mean values were significantly different ($t = -7.133$; $P < 0.05$), individual pairs are joined by lines: 1. *Chasmina tibialis* (Ct) × *Callopistria alticola* (Ca); 2. *Chrysodeixis eriosoma* Ce) × *Chrysodeixis collardi* (Cc); 3. *Leucocosmia nonagrica* (Ln) × *Callopistria steevei* (Cs); 4. *Mocis trifasciata* (Mt) × *Bastilla insularum* (Bi); 5. *Achaea janata* (Aj) × *Hydrillodes crispipalpus* (Hc).

tibialis × *Callopistria alticola*; (ii) *Leucocosmia nonagrica* × *Callopistria steevei*; (iii) *Mocis trifasciata* × *Bastilla insularum*; (iv) *Chrysodeixis eriosoma* × *Chrysodeixis collardi*; and (v) *Achaeta janata* × *Hydrillodes crispipalpus*. The results of the paired-sample *t*-tests (Fig. 1b) reveal that adventives significantly reduced their flight times when exposed to ultrasound compared with endemics (adventives: $-51.8 \pm 15.3\%$, endemics: $59.9 \pm 31.1\%$; $t = -7.133$; $P < 0.05$). Mean effect sizes were computed for the 12 species tested in the flight trials and were also found to be significantly different (adventives: 1.37, endemics: 0.39; $t = 3.272$; $P < 0.05$).

A reanalysis of the auditory data of Fullard (1994) confirms that the ears of endemic species differ from those of adventives only in their high frequency (>45 kHz) sensitivity (Fig. 2). The median best frequencies [BF, stimulus frequency (kHz) requiring the
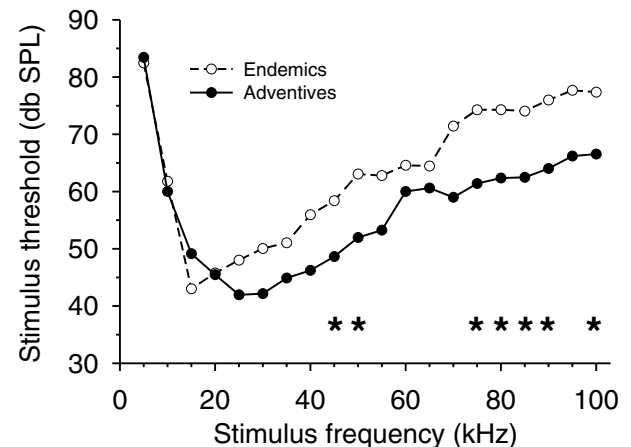
(b)

Using the noctuid subfamily phylogeny of Speidel *et al.* (1996), the following matched-pair adventive vs. endemic species comparisons were made: (i) *Chasmina*

Fig. 2 The median auditory sensitivity curves published in Fullard (1994) of the adventive and endemic moths used in the flight trials of the current study following the taxonomic revisions determinations of Orhant (2002, 2003). Asterisks indicate significantly different threshold values (Mann–Whitney *U*-tests, significance at $P < 0.05$).

lowest intensity to elicit neural threshold] of endemics (BF = 25.0, range: 15.0–35.0) are the same as those of adventives (BF = 27.5, range: 15.0–35.0) (Mann–Whitney *U*-test: $t = 24.0$, $P > 0.05$) and are values within the bandwidths used by most aerially hawking echolocating bats (Fenton *et al.*, 1998).

Discussion

Our study demonstrates that in the anciently bat-free environment of Tahiti, endemic moths possess ears superficially similar to those of adventive species but which evoke significantly reduced ASRs. Our results suggest that taxa that have recently immigrated to bat-free habitats have retained normal auditory sensitivities and flight defences, whereas endemic moths have decoupled their sensory output from the neural pathways that previously evoked this behaviour thus rendering their ears functionally vestigial. We stress that it is not the behaviour of flight interruption that has been lost in Tahitian endemics (these moths are presumably still capable of altering their flight in response to other stimuli) but rather it is the method by which this behaviour is evoked that has regressed (i.e. the ASR).

We suggest that the extinction of the ASR in endemic Tahitian moths represents a case of evolutionary regression that may be directional from the sensory to motor level (as suggested by the partial deafness of the ears) or nondirectional via a reduction in the interneuronal pathways which previously allowed communication between sensory (ears) and motor (flight musculature) systems. As bats exist east and west of the islands of French Polynesia, we assume that, wherever they originated, the progenitors of Tahitian endemic moths possessed fully integrated anti-bat flight responses before they arrived on their new, bat-free habitat. It was then the sudden and total absence of bats that immediately removed the selection pressure maintaining the connection of the ears to the motor patterns that formally generated the ASR. We suggest that other studies to date have revealed sensoribehavioural regression in moths (Heitmann, 1934; Cardone & Fullard, 1988) and grasshoppers (Arbas, 1983a; Riede *et al.*, 1990) that has occurred in a motor to sensory direction, as these changes resulted first from the extinction of a behaviour (flight or singing) which then reduced the need for the sense that originally accompanied it. Another example of a sensory to motor directed regression would be in blind cave animals (Green & Romero, 1997; Li & Cooper, 2002) but in these cases the behaviours that were previously visually evoked have remained and are now activated by other sensory organs (e.g. extraocular photoreceptors) or modalities (e.g. antennae). However, common vampire bats have maintained both the sensory structures (functional taste buds) and motor responses (rapid voiding of the body of food) normally necessary for acquiring taste aversions but appear to have lost the neural substrates responsible for predisposing animals to readily associate novel foods with gastrointestinal distress (Ratcliffe *et al.*, 2003).

The sensoribehavioural disintegration of Tahitian moths suggests that an early result of the release of selection pressure is the decoupling of sensory input from the neural pathways that evoke behaviour. Neuroanatomical examinations of vestigial networks in other insects suggest that the cellular events underlying this decoupling could reside in the sensory neurons [e.g. reduction in receptor cell terminal arborizations (Arbas, 1983a; Riede *et al.*, 1990)] and/or in the interneurons that process these inputs (Arbas, 1983b). Roeder (1974) proposed that the anti-bat flight defences of noctuid moths are bimodal with the most sensitive auditory cell (A1) evoking controlled flight away from an approaching bat and the less sensitive cell (A2) activating the sudden erratic flight which constitutes the ASR. It is therefore possible that the extinction of ASR in Tahitian moths may be the result of a single regressive event at the level of A2 cell. We propose that a comparison of the sensory neurons and interneurons that elicit defensive flight in bat-exposed moths (Boyan & Fullard, 1986; Boyan *et al.*, 1990) to homologous neurons in Tahitian moths will assist in understanding the neurological changes that occur during regressive evolution.

Acknowledgments

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