

Auditory sensitivity of Hawaiian moths (Lepidoptera: Noctuidae) and selective predation by the Hawaiian hoary bat (Chiroptera: *Lasiurus cinereus semotus*)

James H. Fullard

Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, Canada L5L 1C6
(jfullard@credit.erin.utoronto.ca)

The islands of Hawai'i offer a unique opportunity for studying the auditory ecology of moths and bats since this habitat has a single species of bat, the Hawaiian hoary bat (*Lasiurus cinereus semotus*), which exerts the entire predatory selection pressure on the ears of sympatric moths. I compared the moth wings discarded by foraging bats with the number of surviving moths on the island of Kaua'i and concluded that the endemic noctuid *Haliophyle euclidias* is more heavily preyed upon than similar-sized endemic (e.g. *Agrotis diplosticta*) and adventive (*Agrotis ipsilon* and *Pseudaletia unipuncta*) species. Electrophysiological examinations indicated that, compared with species less preyed upon, *H. euclidias* has lower auditory sensitivities to the bat's social and echolocation calls, which will result in shorter detection distances of the bat. The poor ears of *H. euclidias* suggest that this moth coevolved with the bat using non-auditory defences that resulted in auditory degeneration. This moth now suffers higher predation because it is drawn away from its normal habitat by the man-made lights that are exploited by the bat.

Keywords: noctuid moths; bats; auditory ecology; Pacific

1. INTRODUCTION

Most nocturnal Lepidoptera (e.g. moths) possess ears that enable them to detect the echolocation calls of aerially hunting, insectivorous bats (Roeder 1967; Surlykke 1988; Fullard 1998) and the main selective force that determines the sensitivity of their ears is the acoustic design of those calls (Roeder 1970; Fullard 1988). While most terrestrial habitats in the world present bat communities with many insectivorous species (Fullard & Belwood 1988), the islands of Hawai'i are home to only one, the Hawaiian hoary bat, *Lasiurus cinereus semotus* (Whitaker & Tomich 1983; Tomich 1986; Morales & Bickham 1995; Jacobs 1996). This bat, like the North American subspecies *Lasiurus cinereus cinereus*, feeds heavily on moths (Black 1972; Whitaker & Tomich 1983; Belwood & Fullard 1984; Barclay 1985; Jacobs 1999). Therefore, the entire acoustic predatory selection pressure of this habitat consists of the two vocalizations emitted by *L. c. semotus* while it hunts, namely its 10 kHz social call and its 28 kHz echolocation signal (Belwood & Fullard 1984) and endemic moths (i.e. those that have coevolved with this bat) have ears that are sensitive to both of these calls (Fullard 1984).

Belwood & Fullard (1984) reported that, while moths observed at a site on the Hawaiian island of Kaua'i exhibited defensive flight responses to the attacks of the bat, certain species (e.g. *Haliophyle euclidias*) were more heavily preyed upon. Since Barclay *et al.* (1999) and Jacobs (1999) have reported that the Hawaiian bat is flexible in its echolocation and foraging behaviour, it may selectively prey upon particular moths, the auditory ability of which is deficient relative to less preyed upon moths. The rarefied bat environment of Hawai'i provides a unique opportunity for testing whether predators can exploit the sensory limitations of insects and feed upon them.

2. MATERIAL AND METHODS

(a) Location and animals

This study was conducted in Kōke'e State Park, western Kaua'i from 5 July to 5 September 1987 and from 1 to 5 June 1999 (State of Hawai'i Division of Forestry and Wildlife endorsement no. FHM99-8). Moths were hand collected from security lights surrounding the radar station operated by the 150th Air National Guard, a site used nightly by hunting *L. c. semotus* (Belwood & Fullard 1984). The radar station is within the park and is surrounded by a native 'ōhi'a-lehua (*Metrosideros* spp.) forest. Moths were identified by using the lists in Zimmerman (1958) and Nishida *et al.* (1992) and by comparisons with specimens and vouchers previously deposited (Fullard 1984) in the Bishop Museum (Honolulu).

(b) Moth auditory analyses

The auditory examinations were similar to those described in Fullard (1984) and used stainless steel hook electrodes for extracellularly monitoring the moths' auditory nerve responses to pulsed acoustic stimuli (generated by a Hewlett-Packard 3311A function generator (Hewlett-Packard Company, Cupertino, CA, USA) and shaped by a Coulbourn envelope shaper (Coulbourn Instruments, Allentown, PA, USA)) (variable duration and intensity with 1 ms rise/fall time), which were broadcast from a high-frequency speaker (Technics EAS10TH400B; Technics Instruments, Secaucus, NJ, USA). Stimulus intensities were measured by placing a microphone (Brüel & Kjær type 4135) in the sound field of the speaker and directly reading the sound pressure levels (dB SPLs) from equal amplitude continual tones before pulsing was applied. Two stimulus frequencies were used for this study, namely those of the average peak frequencies of *L. c. semotus*'s echolocation call (28 kHz) and social call (10 kHz) (Belwood & Fullard 1984). In order to compare auditory sensitivities, traditional physiological measurements were made of the moths' auditory responses, namely their auditory receptor thresholds (determined as that

Table 1. *List of the moths and wings taken from the foraging site of L.c. semotus on Kōke'e*

(‘All nights’ refers to the five nights that wings were collected and ‘mutual nights’ refers to the three nights when wings and moths were collected simultaneously. The number of items collected and the percentage of this total that this number represents are given for each night category. The following species name changes indicated refer to nomenclature revisions made since Fullard (1984). The data for *A. diplosticta* are revised from *Agrotis hephaestaea* in Fullard (1984) and those for *Athetis thoracica* are revised from *Elydna nonagraca* in Fullard (1984). All species in the genus *Eupithecia* are endemic (Nishida *et al.* 1992).)

species	status	all nights				mutual nights			
		moths		wings		moths		wings	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Noctuidae									
<i>Agrotis diplosticta</i>	endemic	2	6.1	0	0.0	2	6.1	0	0.0
<i>A. dislocata</i>	endemic	3	9.1	0	0.0	3	9.1	0	0.0
<i>A. ipsilon</i>	adventive	5	15.2	4	7.8	5	15.2	2	10.0
<i>A. thoracica</i>	adventive	1	3.0	3	5.9	1	3.0	1	5.0
<i>Chrysodeixis eriosoma</i>	adventive	1	3.0	0	0.0	1	3.0	0	0.0
<i>Haliophyle euclidias</i>	endemic	1	3.0	22	43.1	1	3.0	10	50.0
<i>Helicoverpa zea</i>	adventive	0	0.0	1	2.0	0	0.0	0	0.0
<i>Lycophotia porphyrea</i>	adventive	9	27.3	4	7.8	9	27.3	0	0.0
<i>Peridroma cinctipennis</i>	endemic	3	9.1	2	3.9	3	9.1	0	0.0
<i>Pseudaletia unipuncta</i>	adventive	2	6.1	4	7.8	2	6.1	3	15.0
Geometridae									
<i>Eupithecia</i> sp.	endemic	2	6.1	0	0.0	2	6.1	0	0.0
<i>E. monticolens</i>	endemic	0	0.0	1	2.0	0	0.0	0	0.0
<i>Scotorythra euryphaea</i>	endemic	1	3.0	1	2.0	1	3.0	0	0.0
<i>S. kuschei</i>	endemic	0	0.0	1	2.0	0	0.0	1	5.0
<i>S. rara</i>	endemic	3	9.1	8	15.7	3	9.1	3	15.0

intensity required to elicit two spikes per stimulus pulse) and intensity–response relationships (number of auditory receptor spikes per stimulus pulse). Statistical analyses were performed on the data using non-parametric tests following examinations of normality (D’Agostino test) and homoscedasticity (χ^2 -test) (Zar 1984) and are reported with a significance level of $p < 0.05$.

(c) *Bat recordings*

Echolocation and social vocalizations were recorded from bats as they foraged around the security lights of the radar station with a Brüel & Kjær type 4135 microphone and type 2204 measuring amplifier (Brüel & Kjær, Naerum, Denmark) and RACAL Store 4DS tape recorder (RACAL Instruments, Harrow, Middlesex, UK). Calls were later analysed with a Nicolet 100A fast-Fourier transform mini-analyser. The bats’ acoustic assemblage spectrum (Fullard & Belwood 1988) was generated by averaging the digitized spectra of all of the vocalizations recorded from five bat interactions (*ca.* 200 calls).

(d) *Bat foraging*

The prey base available to foraging bats was estimated by collecting all the moths that were drawn to a security light on the periphery of the radar station where the bats hunted. Which moths were preyed upon by the bats was estimated by collecting all of the moth wings discarded by hunting bats (*cf.* Belwood & Fullard 1984; Jacobs 1999) until 02.00 each night during the 1999 portion of the study.

3. RESULTS

(a) *Bat foraging*

Between two and six bats began foraging each night at 19.30–20.00 and continued to hunt (except during periods

of heavy wind or rain) after I left the site at 02.30. Table 1 lists the identities of the live moths that were collected near to where *L. c. semotus* foraged and the wings that were discarded by the bats as they hunted. The number of moths that the wings represented was estimated by treating forewings (hindwings were not used) that differed in length by more than 10% or were of dissimilar colours and patterns as belonging to different individuals. In spite of its Hawaiian location, the high altitude (1280 m) of the Kōke’e site renders it an inhospitable locale at night, with temperatures often below 10 °C, accompanied by intermittent rain, wind and fog. In spite of the low numbers of insects attracted nightly to the lights in these conditions, bats hunted almost continually and attacked any moth near to them. Most of the moths that I observed being attacked responded with evasive flight patterns (*cf.* Roeder 1962) but the moth versus wing comparisons in table 1 indicate that, as reported in Belwood & Fullard (1984), the endemic noctuid *H. euclidias* was more heavily preyed upon than other similar-sized moths, both adventive and endemic. Three of the noctuid moths, the adventive species *Agrotis ipsilon* and *Pseudaletia unipuncta* and the endemic *Agrotis diplosticta* (the wings of which were never found) were encountered less in the wing remains of the bats and were used as the subjects of the auditory comparisons with *H. euclidias*.

(b) *Moth auditory analyses*

The Kauaian noctuid moths that I examined exhibited typical auditory responses that were attributable to two receptors, namely the more sensitive A_1 cell and the less sensitive A_2 cell (Roeder 1967). All moths had characteristically low auditory nerve baseline activities

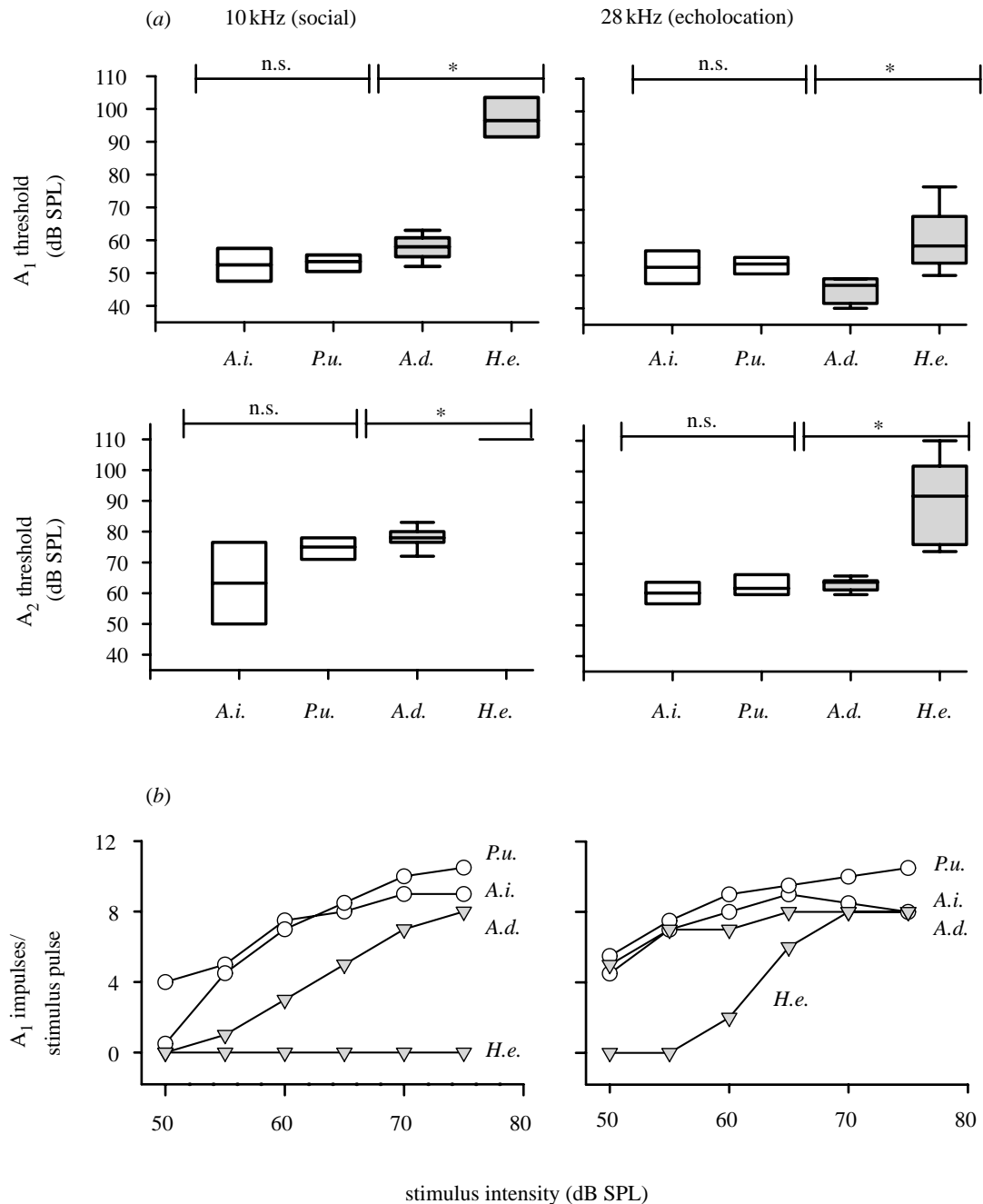


Figure 1. (a) Box plots (the boundary of the box closest to zero is the 25th percentile, the line within the box is the median, the boundary of the box farthest from zero is the 75th percentile and the whiskers above and below the box are the 90th and 10th percentiles, respectively) of the responses of the two auditory receptors (A_1 and A_2) of the adventive moth species (open boxes) (*A.i.*, *A. ipsilon* ($n=2$) and *P.u.*, *P. unipuncta* ($n=4$)) and endemic species (shaded boxes) (*A.d.*, *A. disploticta* ($n=5$) and *H.e.*, *H. euclidias* ($n=5$)) to the two mean vocalization frequencies of the Hawaiian bat (social 10 kHz and echolocation 28 kHz): n.s., not significant; *, significant. (b) The intensity/response curves of Kauaiian moth A_1 auditory receptors to 10 ms stimulus pulses at the Hawaiian bat's social and echolocation frequencies.

and the responses of each receptor cell could be easily distinguished by eye. Figure 1a illustrates the median auditory thresholds for the A_1 and A_2 receptors of the four moth species in the auditory comparisons. Separate comparisons were made of adventive and endemic moths in order to make use of the isolated evolutionary environment of Hawai'i (Simon *et al.* 1984) and I report the median thresholds since some insects tested were non-responsive to the highest intensity presented to them. The deafness of these moths necessitated an assignment of

110 dB as an arbitrary threshold with subsequent non-parametric statistical analyses. Figure 1a indicates that the moths in this study had A_1 -cell thresholds ranging from 48 to 109 dB at *L. c. semotus*'s social call peak frequency (10 kHz) and thresholds of 39–77 dB at its echolocation call peak frequency (28 kHz). The A_2 -cell thresholds were *ca.* 20 dB higher, ranging from 50 to 110 dB (i.e. no threshold attainable) at the social peak frequency and from 57 to 110 dB at the echolocation peak frequency. The thresholds of the A_1 and A_2 cells did not differ significantly

between the adventive species at either frequency (Mann–Whitney rank sum tests (SigmaStat 2.0), A_1 at 10 kHz $T=7.0$ and at 28 kHz $T=10.5$ and A_2 at 10 kHz $T=6.0$ and at 28 kHz $T=6.0$). However, when comparing the two endemic species, the A_1 - and A_2 -cell thresholds at both frequencies were significantly higher in the prey species *H. euclidias* than the non-prey species *A. diplosticta* (A_1 at 10 kHz $T=15.0$ and at 28 kHz $T=15.0$ and A_2 at 10 kHz $T=15.0$ and at 28 kHz $T=15.0$).

In order to examine whether the low sensitivities of *H. euclidias* were further exhibited at sound levels above its threshold, intensity/response relationships were derived. The curves of figure 1*b* represent A_1 -cell responses to pulsed stimuli (duration 10 ms with 1 ms rise or fall time and two pulses s^{-1}) of increasing intensity at the social and echolocation call peak frequencies. Both of the adventive species and also the endemic non-prey species *A. diplosticta* exhibited a rising response to intensity at 10 kHz with resultant plateaux at 60–65 dB while the endemic prey species *H. euclidias* exhibited no response to any intensity. All species exhibited rising responses at 28 kHz although the plateau phase was much less for *H. euclidias*.

The maximum detection distances (MDDs) that a moth with a given auditory threshold has for a bat call can be estimated (Fenton & Fullard 1979; Surlykke 1988) by using the sound attenuation curves of Griffin (1971) and Lawrence & Simmons (1982). Since the natural vocalization intensities of *L. c. semotus* are unknown, the curves for each moth species in figure 2*a* plot their MDDs against a range of call decibels. Using median A_1 -cell thresholds for each species (figure 1), the curves indicate that, for a vocalization intensity of 100 dB (Kick & Simmons 1984), the non-prey endemic species *A. diplosticta* possessed MDDs greater than 15 m to the bat's echolocation call frequency and 7 m to the social call frequency. The prey species *H. euclidias* possessed lower MDDs to the echolocation call frequency (< 10 m) and had a negligible response (< 1 m) to the social call frequency.

(c) *Bat vocalizations*

Figure 2 illustrates the spectral characteristics of the vocalizations recorded from the bats on Kaua'i. The echolocation frequencies are peaked between 28 and 31 kHz (inset in figure 2*a*) and are more consistent than those of the social vocalizations. As described by Belwood & Fullard (1984), when hunting bats encounter each other they engage in vigorous pursuits with one or both emitting social (putatively territorial), human-audible calls (cf. Barclay (1985) for similar behaviour in the North American subspecies *L. c. cinereus*). The inset in figure 2*a* illustrates a typical 10 kHz social call. In addition to these calls, I also recorded intermediate calls that the bats emitted as they approached each other. As the bats began their vocal displays, they dropped the peak frequency of each successive call (five to nine calls) from that of their echolocation call until a final peak frequency of ca. 10 kHz was reached. When the spectra of all the vocalizations (echolocation, social and intermediate) recorded during an interaction were averaged together, an assemblage spectrum (Fullard & Belwood 1988) resulted with acoustic power from 10 to 30 kHz (figure 2*b*). Since it was impossible to control for the orientations of the bats as they vocalized, this assemblage spectrum does not

represent their total acoustic output. However, it does represent a realistic spectrum from the moths' perspective since the positions of the bats were as unpredictable to their ears as to my recording microphone. The median audiogram of a sample of noctuid moths (Fullard 1984) was superimposed upon this spectrum in order to illustrate that these moths were tuned between the two primary peak frequencies of the bats' vocalizations.

4. DISCUSSION

Most moths that fly in the same airspace as hunting bats avoid predation by using their ears, which are syntonized (frequency matched), with the predatory vocalizations of those bats (Roeder 1970; Fullard 1988). Although these moths are under intense predation potential, the efficacy of their auditory defence is such that they occur less in the diets of individual bats. On Kaua'i, adventive moths such as *A. ipsilon*, *P. unipuncta* and *A. diplosticta* were found more at collecting lights than were represented in the wing remains left by foraging bats and I conclude that these species are less preyed upon by *L. c. semotus* because of the sensitivity of their ears. Whereas it is difficult to know the evolutionary predatory past of adventive Hawaiian moths, endemic species can be assumed to have been exposed to only the isolated influence of *L. c. semotus*. Using traditional physiological measurements my results demonstrated that *H. euclidias* is significantly deafer than the other endemic species tested, i.e. *A. diplosticta*, and I suggest that its poorer hearing is one reason for its higher predation. Both species have similar wingspans and body shapes so size selectivity by the bat (Barclay 1985) is not likely to play a significant role. As an alternative explanation, Zimmerman (1958), quoting Perkins (1913), described the late flight times (after 23.30) of (presumably) *H. euclidias* and it is possible that bats feed more heavily on this moth later in the night although I saw no greater numbers of this species up to the time (02.30) when I left the Kōke'e site.

Assuming that the endemic status of *A. diplosticta* and *H. euclidias* means that these species have existed with the Hawaiian bat for evolutionarily significant amounts of time, it is difficult to explain, from an adaptive standpoint, why *H. euclidias* should be deafer than *A. diplosticta* and suffer higher predation as a result. The short reproductive life of most Lepidoptera implies that selection will favour individuals that maximize their time flying in search of mates and/or oviposition sites (Fullard *et al.* 1997; Fullard & Napoleone 2001). Although ultrasound-sensitive ears allow most moths to fly more continually during the night, there are non-auditory behavioural defences that can reduce an insect's exposure to hunting bats. Certain earless moths exhibit reduced or concealed flight (Roeder 1974; Morrill & Fullard 1992; Rydell 1998; Jensen *et al.* 2001) while others have adopted diurnal flight (Fullard *et al.* 1997; Surlykke *et al.* 1998) and now possess degenerate ears. If *H. euclidias* uses one of these alternative defences it could explain its present-day auditory insensitivity. Although *H. euclidias* is not diurnal, Zimmerman's (1958) observation that its host plants are ferns suggests that adults normally fly low to the ground, an earless moth behaviour which would isolate them from hunting bats. On the other hand, the host plants of

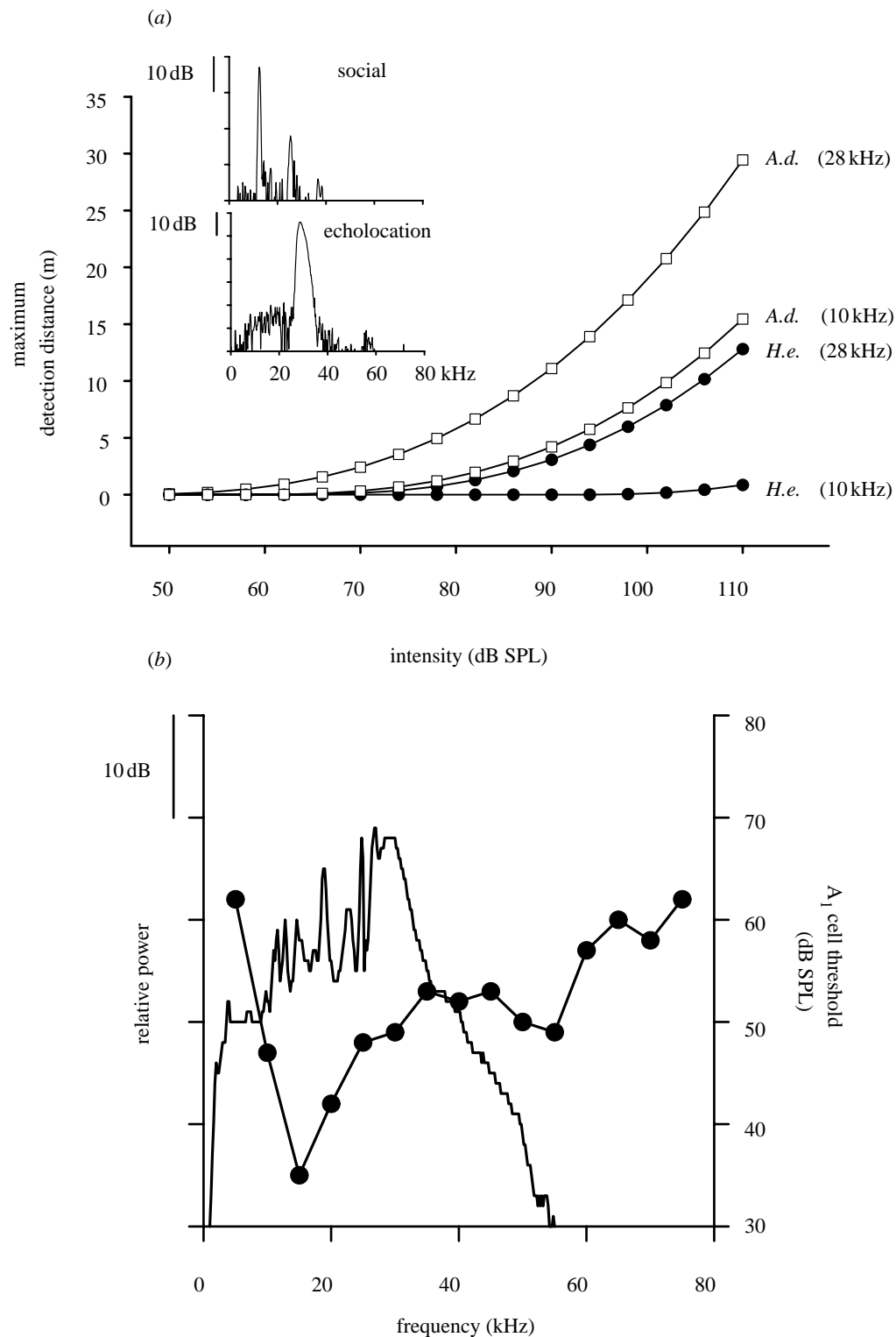


Figure 2. (a) MDDs of the Hawaiian bat's two vocalization frequencies (insets) for the Kauaian endemic moths *A. diplosticta* (*A.d.*) and *H. euclidius* (*H.e.*). The curves use the moths' median A_1 -cell thresholds for each vocalization frequency (figure 1a) and attenuation factors for the bat's signals at a relative humidity of 80% (Griffin 1971). (b) The acoustic assemblage spectrum computed after averaging the spectra of ca. 200 echolocation, social and intermediate vocalizations. Superimposed on this spectrum is the median audiogram of 27 Kauaian noctuid moths (from Fullard 1984).

A. diplosticta are trees, which would predispose this species to higher, more bat-exposed flight. The *H. euclidius* that I collected at lights may have been drawn there away from their normal habitat (i.e. the native forest surrounding the site) and, consequently, suffered high levels of

predation from bats. These results therefore serve as a cautionary note for researchers wishing to extrapolate evolutionary trends from the foraging behaviour of bats studied at lights or other areas that may contain unnatural distributions of insect prey.

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