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## Research

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<sup>†</sup>Dedicated to the late Prof. James H. Fullard.

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## Animal behaviour

# If a bird flies in the forest, does an insect hear it?<sup>†</sup>

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Birds are major predators of many eared insects including moths, butterflies, crickets and cicadas. We provide evidence supporting the hypothesis that insect ears can function as 'bird detectors'. First, we show that birds produce flight sounds while foraging. Eastern phoebes (*Sayornis phoebe*) and chickadees (*Poecile atricapillus*) generate broadband sounds composed of distinct repetitive elements (approx. 18 and 20 Hz, respectively) that correspond to cyclic wing beating. We estimate that insects can detect an approaching bird from distances of at least 2.5 m, based on insect hearing thresholds and sound level measurements of bird flight. Second, we show that insects with both high and low frequency hearing can hear bird flight sounds. Auditory nerve cells of noctuid moths (*Trichoplusia ni*) and nymphalid butterflies (*Morpho peleides*) responded in a bursting pattern to playbacks of an attacking bird. This is the first study to demonstrate that foraging birds generate flight sound cues that are detectable by eared insects. Whether insects exploit these sound cues, and alternatively, if birds have evolved sound-reducing foraging tactics to render them acoustically 'cryptic' to their prey, are tantalizing questions worthy of further investigation.

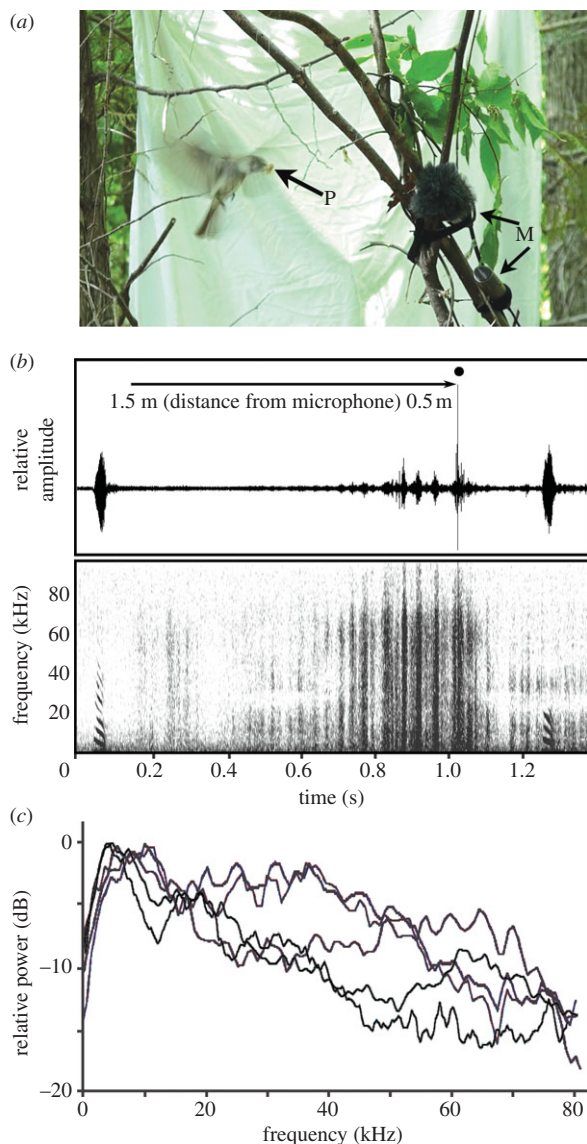
## 1. Introduction

Most eared insects, including moths, butterflies, grasshoppers and crickets, are consumed by birds [1,2]. While insects have evolved well-documented anti-avian strategies, including camouflage, startle and aposematism [3], the role of hearing in detecting foraging birds has received little consideration [4]. If insect ears function as 'bird detectors', one prediction is that foraging birds produce acoustic cues. Our first objective was to record sounds produced by two insect-eating birds: the Eastern phoebe (*Sayornis phoebe*), a flycatcher that captures insects by aerial hawking, and the chickadee (*Poecile atricapillus*), which hawks aerially and gleans from surfaces [5]. Another prediction is that insect ears can detect bird flight sounds. Our second objective was to perform neurophysiological recordings from the ears of moths and butterflies—representing insects with high- and low-frequency hearing, respectively—during bird flight playbacks.

## 2. Material and methods

### (a) Flight sound recordings

Flight sounds of phoebes were recorded at Queen's University Biology Station (44°34'N, 76°19'W) near Chaffey's Lock, Ontario, Canada (May–August, 2009–2010; CCAC Permit no. AUP B10-15). Noctuidae moths were tethered with cotton thread and suspended from a branch in clear view (less than 10 m) of a phoebe nest. Microphones with different frequency characteristics (Earthworks QTC40, Milford, NH, USA (4 Hz–40 kHz ± 1 dB); Avisoft Acoustics CM16 Berlin, Germany (custom-manufactured 5–200 kHz ± 6 dB)) were fastened to a branch approximately 50 cm from the insect (figure 1a) and connected to a Fostex-FR2 recorder (Akishima, Tokyo, Japan; 16-bit .wav files sampled at 192 kHz). Two video cameras (Sony Steady Shot DCR-TRV19) were positioned within 5–10 m at 90° angles, and sounds were recorded by one camera using a microphone (Sony ECM-MS907).



**Figure 1.** (a) Video frame showing a phoebe capturing a tethered moth prey (P) and the location of microphones (M). (b) Waveform and spectrogram of flight sounds as the bird approaches and attacks a moth. The point of capture is marked with a circle. Two calls from a neighbouring bird are included at either end for comparison. (c) Power spectra of flight sounds from five individual birds (Avisoft microphone). (Online version in colour.)

Wing-beat frequency (WBF) was measured from a 500 ms segment of the sound file prior to time of capture. Spectral analysis was performed on 10 wing-beat cycles prior to capture (512 pt dFFT with Hanning Window; frequency resolution of 188 Hz). Sound levels of bird flight at various distances were estimated by comparing recordings against calibrated tones (see the electronic supplementary material, methods S1). Sounds were analysed using RAVEN PRO v. 1.3.

Chickadees were recorded at Mer Bleue Bog (45°22' N 75°30' W) in Ottawa, Ontario (January–May, 2009–2010; NCC permit no. 10006). Birds approached seed in the outstretched hand of the experimenter while the recording microphone (as for phoebe) was directed at the bird (electronic supplementary material, figure S2). Although chickadees were not capturing insects, this method is similar to that used to glean insects from bark or foliage [5]. Other details are as described for the phoebe (see also the electronic supplementary material, methods S1).

### (b) Neurophysiology

Extracellular nerve recordings from moths and butterflies were made in response to bird flight playbacks. Noctuoidea moths

(*Trichoplusia ni*) were purchased from the Canadian Forest Service and Nymphalidae butterflies (*Morpho peleides*) from London Pupae Supplies (Permit-2011-01618). Recordings and audiograms of the moth (3N1b) and butterfly (2N1cNIII) auditory nerves were conducted using established methods (see electronic supplementary material, methods S1). Flight sounds of foraging phoebes were used for playbacks. Preparations were exposed to sound clips of four flight cycles (approx. 200 ms) played at different sound levels (for moth preparations) and full attacks (approx. 1–3 s; for moth and butterfly preparations) broadcast using an Avisoft Scan-Speak (1–120 kHz) and Avisoft USG Player 116 (see the electronic supplementary material, methods S1).

## 3. Results

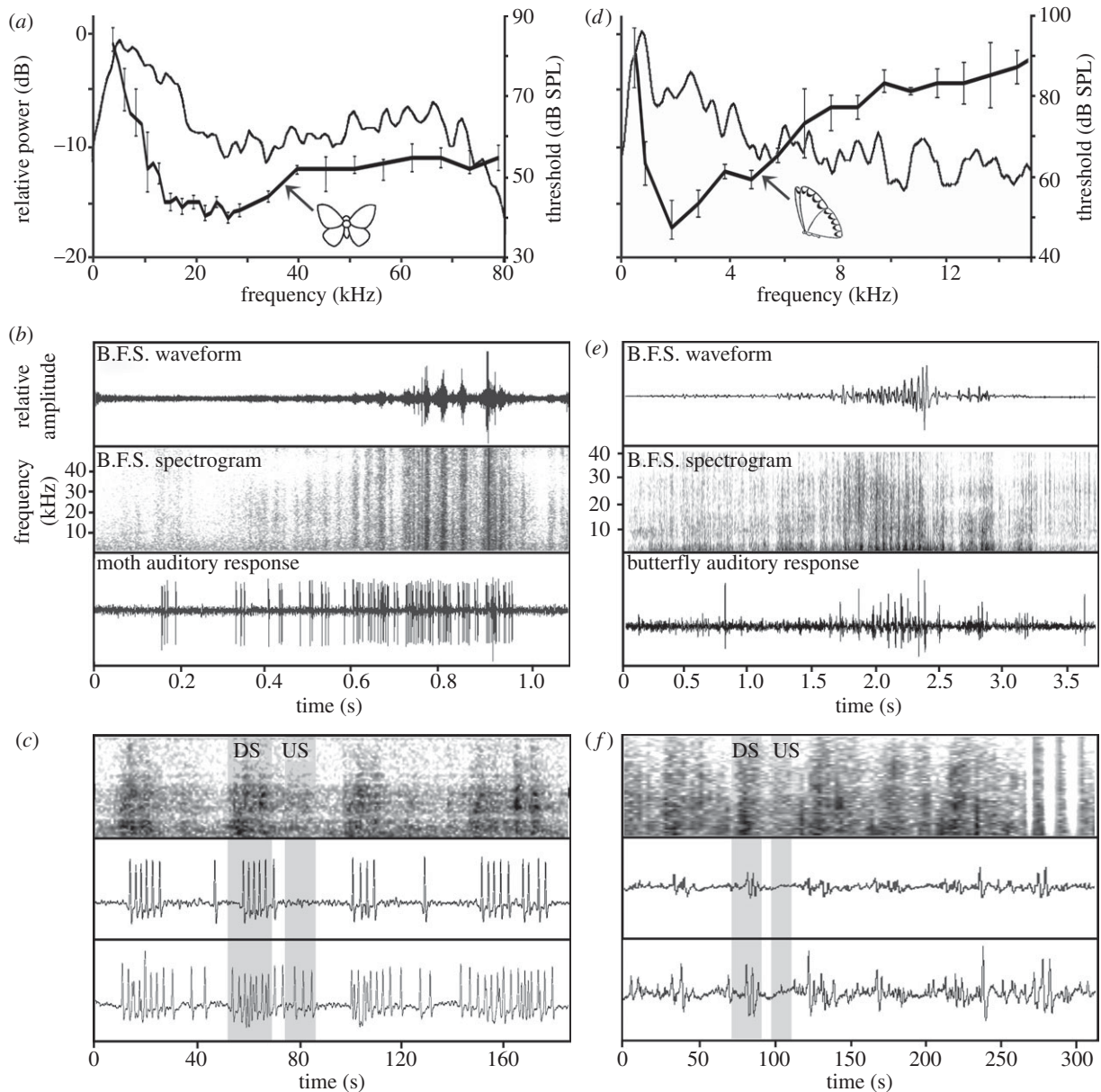
Flight sounds and videos were recorded from 32 attacks on tethered moths by five nesting phoebe pairs. Most attacks (30/32) were categorized as 'aerial hovering', whereby the bird approached the insect and hovered before attacking (electronic supplementary material, movie S3). Sounds were pulsed owing to cyclic wing beats (WBF  $18.5 \pm 0.19$  Hz (mean  $\pm$  s.e.m.);  $n = 8$  birds,  $N = 21$  attacks), with the down-stroke louder than the up-stroke (figures 1b and 2). Sounds had a peak frequency of  $863.2 \pm 101.5$  Hz (mean  $\pm$  s.d.) ( $n = 5$ ) and were broadband ( $41.0 \pm 20.2$  kHz at  $-10$  dB below peak) with significant energy extending into the ultrasound (figures 1 and 2). Sound levels at distances of 120 and 15 cm were estimated to be 64 and 79 dB SPL (re. 20  $\mu$ Pa root mean squared) (at 1 kHz) and 54 and 69 dB SPL (at 25 kHz), respectively ( $n = 5$ ). Of the remaining 2/32 trials, in one case, the phoebe hovered for several seconds as it gleaned the moth from a leaf; in the other, the bird performed a 'fly through' attack, with no hovering, and performed so quickly (less than 100 ms) that little sound was recorded.

Flight sounds of foraging chickadees were similar to those of phoebes; they were pulsed (WBF  $20.7 \pm 2.5$  Hz) (mean  $\pm$  s.e.m.; electronic supplementary material, figure S2;  $n = 11$ ) and broadband ( $49.3 \pm 17.7$  kHz at  $-10$  dB below peak), with sound levels at distances of 15 and 120 cm estimated to be 84 and 66 dB SPL (at 1 kHz) and 78 and 60 dB SPL (at 25 kHz), respectively ( $n = 5$ ).

### (a) Neurophysiology

The frequency range of moth hearing overlaps with the high frequency component of bird flight (figure 2a). Based on sound level measurements of bird flight and hearing thresholds of the moth at 25 kHz, we estimate that the moth can detect a bird at distances of at least 2.5 m. A1 cells of all moths ( $n = 16$ ) responded to playbacks in a bursting pattern that corresponded to the bird's wing beats (figure 2b,c). As intensity increases, A1 spike rates increase (Pearson correlation:  $R^2 = 0.94$ ,  $p = 0.001$ ) ( $n = 5$ ) and interspike intervals decrease to 2.5 ms (table 1). Below 53 dB SPL (at 25 kHz), A1 responds in a bursting manner to only the down-stroke; at higher levels, A1 responds to both up- and down-strokes, and A2 is recruited (figure 2c and table 1).

Butterfly hearing overlaps with the lower frequency components of bird flight sounds (figure 2d). The compound action potential of the NIII auditory nerve responded in a bursting pattern to playbacks of an approaching bird, with an amplitude increase of  $256 \pm 135\%$  (mean  $\pm$  s.e.m.;  $n = 5$ ) from the beginning to the end of the playback (representing a dynamic range of approx. 20 dB over a time period of 2.5 s). Based on sound level measurements of bird flight and hearing



**Figure 2.** Auditory nerve responses to bird flight sounds. (a) Representative power spectrum of phoebe flight sound (Avisoft microphone) superimposed on the threshold curve (median and quartiles) of the moth A1 cell ( $n = 5$ ) to show overlap in the frequency domain. (b) Top: bird flight sound (B.F.S.) waveform as the bird approaches prey; middle: corresponding spectrogram; bottom: response of moth auditory cells. (c) Auditory cells responding to four wing-beat cycles (top) played at 10 (middle) and 20 (bottom) dB above threshold of the ear. DS—down-stroke and US—up-stroke of one flight cycle. (d) Representative power spectrum of phoebe flight sound (Earthworks microphone) superimposed on the butterfly audiogram (median and quartiles) ( $n = 5$ ). (e) Compound action potential of butterfly auditory nerve in response to a phoebe approach. (f) Auditory response to six wing-beat cycles (top) played at 10 (middle) and 20 (bottom) dB above threshold.

thresholds of butterflies at 1 kHz, we estimate that these butterflies can detect a bird at distances of at least 2.5 m.

## 4. Discussion

This is the first study to characterize flight sound cues of foraging birds. Previous studies report on wing sonations that function as communication signals [6]. These sounds are associated with specialized feather modifications and kinematics that presumably evolved as modifications of flight. On the flip side, some owls are presumably acoustically cryptic and have evolved specialized feather modifications to reduce sounds while foraging [7]. Whether prey can detect flight sounds of predatory birds had not been tested until now.

Do some insect ears function as ‘bird detectors’? Invertebrates and vertebrates can detect acoustic cues produced

by predators (e.g. caterpillars detect wasp flight [8]; nestlings detect predators walking in leaf litter [9]). Given the strong selective pressure that birds have on insects, and our findings that foraging birds produce sounds, it might be expected that eared insects exploit such cues. We present three arguments supporting the ‘bird detector’ hypothesis. First, bird flight sound frequencies overlap with the hearing of most tympanate insects, including those with sensitivity in the sonic (e.g. cicadas, butterflies and grasshoppers) and ultrasonic (e.g. moths and mantids) [10]. Both butterflies and moths can detect flight sounds within at least a few metres. Interestingly, the moth A1 cell response to bird flight is similar to that proposed to elicit evasive flight manoeuvres (i.e. burst patterns less than 200 ms, and interspike intervals less than 2.6 ms) [11]. Second, there are several insects that possess hearing for which the function is not known, and they could be using their ears for predator detection. Silent

**Table 1.** Response of moth auditory cells to bird flight sound playbacks<sup>a</sup>.

estimated distance to moth <sup>b</sup> (m)	sound level <sup>c</sup> at 25 kHz (dB SPL)	A1 spikes/flight cycle	A1 interspike interval (ms)		A2 spikes/flight cycle	percentage with A2
			down-stroke	up-stroke		
2.0	48	4.8 ± 0.5	5.5 ± 0.5		0	0
1.2	50	7.4 ± 0.7	3.5 ± 0.1		0	0
1.0	53	8.1 ± 0.9	3.5 ± 0.2	4.4 ± 0.2	0	0
0.6	57	14.4 ± 1.0	2.3 ± 0.1	3.5 ± 0.2	1.1 ± 0	45
0.3	61	14.7 ± 0.8	2.5 ± 0.1	3.4 ± 0.1	1.7 ± 0.3	65
0.2	66	21.6 ± 1.1	2.1 ± 0.3	3.8 ± 0.1	2.1 ± 0.2	100

<sup>a</sup>Spike analysis (reporting mean ± s.e.m.) conducted on five moths responding to playbacks of four phoebe flight wing-beats.

<sup>b</sup>Estimated distance between the bird and moth at the sound level indicated.

<sup>c</sup>Based on the loudest components of the playback, represented by the down-stroke.

butterflies and grasshoppers have ears that are broadly tuned and proposed to function in predator detection [12,13]. Moths that have ears tuned to a broad frequency range, or have retained their hearing when removed from the selection pressure of bats, may use their hearing to detect other predators, for instance birds [4,14,15]. In other insects, ears may be tuned to frequencies outside of the call frequency [16,17]. For example, *Cyphoderris* crickets call at 12 kHz, but their ears are most sensitive to 2 kHz, and it is proposed that low frequency hearing is for predator detection [17]. Interestingly, birds are a main predator of this insect [18]. Third, there is evidence that moths may hear and escape from rustling sounds of birds landing on bushes [4], and we suggest that flight sound cues could play a role in mediating this escape response.

Our results provide empirical evidence of bird flight sounds during foraging, and that moth and butterfly ears

respond physiologically to these sounds. Future experiments should explore how eared insects respond behaviourally to bird flight, and whether birds use counter strategies, such as sound-reducing feather modifications or foraging tactics, to avoid detection. Avian predation, like bat predation, may have played a significant role in shaping the evolution of the vast diversity of hearing organs found in insects.

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**Data accessibility.** Raw data files of representative flight sounds and neural responses are available at <http://http-server.carleton.ca/~jyack/>. Owing to the large size of original video and audio files, these are available only upon request.

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