

Can the elongated hindwing tails of fluttering moths serve as false sonar targets to divert bat attacks?

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It has long been postulated that the elongated hindwing tails of many saturniid moths have evolved to create false sonar targets to divert the attack of echolocation-guided bat predators. However, rigorous echo-acoustic evidence to support this hypothesis has been lacking. In this study, fluttering luna moths (*Actias luna*), a species with elongated hindwing tails, were ensounded with frequency modulated chirp signals from all angles of orientation and across the wingbeat cycle. High-speed stereo videography was combined with pulse compression sonar processing to characterize the echo information available to foraging bats. Contrary to previous suggestions, the results show that the tail echoes are weak and do not dominate the sonar returns, compared to the large, planar wings and the moth body. However, the distinctive twisted morphology of the tails create persistent echoes across all angles of orientation, which may induce erroneous sonar target localization and disrupt accurate tracking by echolocating bats. These findings thus suggest a refinement of the false target hypothesis to emphasize sonar localization errors induced by the twisted tails, and highlight the importance of physics-based approaches to study the sensory information involved in the evolutionary arms race between moths and their bat predators. © 2016 Acoustical Society of America.

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I. INTRODUCTION

Many distinct morphological features of animals can be explained by the heavy selection pressure exerted by predation (Cott, 1940). One well-known example is the conspicuous eyespot coloration found on animals across multiple taxa that serve to deflect the attention of visual predators toward non-vital body parts rather than the head (Van Buskirk *et al.*, 2004; Kamoun, 1991; Kjærsmo and Merilaita, 2013; Kodandaramaiah, 2011; Meadows, 1993; Robbins, 1981; Stevens, 2005). A similar strategy has been proposed to explain the presence of elongated, twisted hindwing tails of many saturniid moths (D'Abrera, 1998) as a morphological feature that produces conspicuous echoes to divert the attacks of echolocating bat predators (Barber *et al.*, 2015; Weeks, 1903), which rely on acoustic information in the echo returns to detect, track, and capture prey (Griffin *et al.*, 1960). One representative species of these insects is the luna moth, *Actias luna* [Fig. 1(a)]. A recent behavioral study showed that luna moths with intact hindwing tails survived bat attacks at higher rates than luna moths with ablated tails (Barber *et al.*, 2015). However, the echo-acoustic features of fluttering luna moths and the hypothesized anti-predator mechanism of the elongated twisted tails have not been rigorously investigated.

Acoustic backscattering measurements from tethered insects have been conducted from early on to infer echo information available to foraging bats. Both constant frequency (CF) and frequency modulated (FM) signals have

been used, which correspond to the two primary categories of echolocation calls emitted by insectivorous bats (Denzinger and Schnitzler, 2013). These studies have considered how insect size and wingbeat pattern may contribute to prey detection (Kober and Schnitzler, 1990; Roeder, 1963; Surlykke *et al.*, 1999; Waters *et al.*, 1995) and discrimination by echolocating bats (Emde and Schnitzler, 1990; Kober and Schnitzler, 1990; Moss and Zagaeski, 1994; Simmons and Chen, 1989). Among them, the use of pulse compression processing of broadband FM signals—which delivers enhanced temporal, and thus spatial, echo resolution—was utilized to relate insect morphology with finely resolved echo-acoustic signatures (Moss and Zagaeski, 1994; Simmons and Chen, 1989). However, this technique has not been employed to quantitatively analyze the highly variable echoes from live, fluttering moths with dramatic wingbeat motion and orientation changes. Such investigation is particularly important for elucidating the echo-acoustic effects of moth hindwing tails for bat predators in pursuit of prey in flight.

In this study, we use a combination of broadband sonar processing and high-speed stereo videography to quantitatively characterize the echo-acoustic signatures of live, fluttering luna moth from different angles of ensounding and across the wingbeat cycle. The echo measurements were conducted using linear chirp signals, which allow pulse compression processing for resolving fine echo features. These signals are also similar to those used by bats emitting FM echolocation calls. The observed echo features were attributed to three-dimensional moth morphology reconstructed from synchronized high-speed stereo video recordings. To understand the echo-acoustic

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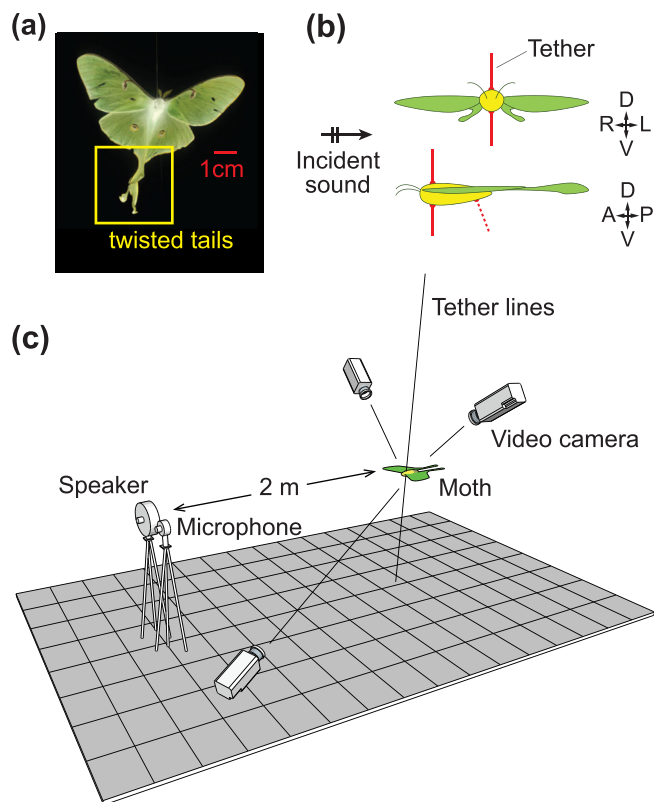


FIG. 1. (Color online) (a) A luna moth (*Actias luna*) with twisted hindwing tails during flight. (b) Moth tether used in the experiment. Solid red lines: primary tether lines used for both the live moths and the recently dead moth specimen. Dotted red line: additional tether line added to the rear abdomen of the recently dead moth specimen to allow motor control of moth orientation. (c) Experimental setup. The ultrasonic frequency modulated (FM) pulse generation and echo recording system and the high-speed video recordings were synchronized during the experiment.

influence of elongated hindwing tails, the experiments were performed on the same individual moths, initially with intact tails and then with the tails ablated.

Using these data, we (1) relate the measured echo-acoustic features of the hindwing tails to their distinctive twisted morphology [Fig. 1(a)] and (2) investigate the widely accepted notion that the tails produce competing sonar targets to divert bat attacks away from the moth body (Barber *et al.*, 2015; Weeks, 1903). Based on studies of the sonar cues used by bats to localize prey (Simmons and Chen, 1989; Simmons, 1973), we develop a set of acoustic-based metrics to evaluate potential anti-predator advantages offered by the elongated tails. We show that the tails may aid in the moth's evasion of bat capture through disruption of accurate target tracking, instead of serving as a separate false sonar target. Our results demonstrate that rigorous examination of the sensory information available to the predators is necessary to fully evaluate evolutionary hypothesis of morphological adaptations for prey survival.

II. MATERIALS AND METHODS

A. Animals

Luna moths (*Actias luna*) were purchased as cocoons from Carolina Biological, Inc. (Burlington, NC) and hatched in a temperature-controlled chamber with a reversed light

cycle. Immediately prior to the experiment, the moths were cold-anesthetized for 7–10 min at -10°C and tethered using thin monofilament (Berkley Trilene, 0.001 in. diameter, 1-lb test) on both the dorsal and ventral sides of the thorax [Fig. 1(b)]. The thorax was partially descaled to facilitate the tether attachment through a mixture of superglue and sodium bicarbonate (baking soda). This simple tether allowed the moth to flutter freely and enabled the collection of echo data from all moth orientations in the lateral plane across the wingbeat cycle. The luna moth hindwing tails were removed half way through the measurement of each moth individual so that echo data were collected both with and without the scattering contributions from the tails. A total of four live luna moths were measured (Table I). A separate set of echo data was also collected by ensoufing a recently dead luna moth specimen from all orientations in the lateral plane. One additional tether line was attached to the rear abdomen of the moth specimen to allow control of its orientation through a stepper motor [Fig. 1(b)].

B. Experimental setup and data acquisition

The experiment was conducted in a carpeted sound-attenuated room ($2.8 \times 2.3 \times 5.2\text{ m}$) lined with sound-absorbing foam (Sonex One, Acoustical Solutions, Inc., VA) in low-light conditions [Fig. 1(c)]. The pulse-echo system consisted of a loudspeaker (Ultra Sound Advice, S56 loudspeaker and power amplifier, London, UK), a microphone (UltraSound Advice, UM3/SP3 microphone and preamplifier), a filter (VBF40, Kemo Limited, Kent, UK), and a National Instrument (Austin, TX) data acquisition system (NI PXIe-1082) running WINDOWS 7. Prior to each experiment, the loudspeaker and microphone were aimed at the tethered location of the moth using a dummy target. The separation between the loudspeaker and the microphone resulted in a 3.5° – 4.3° deviation from the true backscattering at the moth position. The transmit signal was generated using an arbitrary waveform generator (NI PXI-5412) and recorded at the output of the loudspeaker power amplifier via a built-in -40 dB signal sampler.

For experiments with live, fluttering moths, both the transmit signal and microphone output were bandpass-filtered from 10 to 100 kHz and digitized at 1 MHz (NI PXIe-6358). Data from the recently dead moth specimen was collected using a different data acquisition board (NI PXI-6143) at 250 kHz using identical filter settings. The orientation of the dead moth specimen was controlled using a stepper motor (Sparkfun bipolar motor 68 oz.in, Niwot, CO) via a motor controller (STP101, Pontech, Rancho Cucamonga, CA).

The movements and orientation of the moths during experiment were recorded using three high-speed video cameras (Phantom Cameras M310, Vision Research, Wayne, NJ). The video cameras were positioned such that the body and the wings of the moth were visible in at least two cameras at all time [Fig. 1(c)]. The videos were recorded at 250 frames per second with an exposure time of $400\ \mu\text{s}$.

A custom-written LabVIEW program was used to synchronize the acoustic and video data acquisition using a start trigger. The transmit signal was broadcasted 100 times at

TABLE I. Dimensions and sex information of the luna moths used in the experiment. All dimensional measurements were taken from dead moths after echo recordings were completed. The wing length was measured from the tip of the wing to its base on the thorax. The body length was measured from the base of the antennae to the tip of the abdomen. Data were only analyzed if the moth was actively fluttering in the echo recording trial.

Moth #	Sex	Body length (cm)	Left wing length (cm)	Right wing length (cm)	# Trials analyzed (with/without tails)
0117a	Male	2.5	5.3	5.2	10/12
0125a	Male	2.5	5.1	5.0	16/11
0127a	Female	2.3	4.4	4.4	15/12
0220a ^a	Male	2.6	4.6	4.7	20/17
0624p ^b	Female	2.7	5.1	4.7	—

^aData from this live, fluttering moth are presented in Figs. 1–6.

^bData from this recently dead moth specimen are presented in Figs. 3(c) and 3(d).

50 ms interval or 50 times at 100 ms interval in each experimental trial. Only trials in which the moth actively fluttered were included in the data analysis.

C. Three-dimensional reconstruction of moth movement

The posture of the moths during echo measurements was reconstructed in three dimensions using synchronized video images through direct linear transform (DLT) (Hedrick, 2008). The direction of incident sound was identified using a laser pointer positioned at the moth location and aimed at the center of the microphone. Two points located longitudinally on the laser pointer were used to reconstruct a vector representing the direction of incident sound (Figs. 1 and 2). The laser pointer was also aimed at the speaker and the microphone separately to estimate the angle spanned in between from the moth location.

Six locations on the luna moth, including the head (H), tip of the abdomen (B), tips of both wings (W_L and W_R), and tips of both hindwing tails (T_L and T_R), were reconstructed

[Fig. 2(b)]. The orientation of the moth was described by the angle between the vector formed by the head and the tip of abdomen (HB) and the direction of incident sound. The angle between the wings was determined by the angle between the normal vectors of the two planes formed by the head, tip of the abdomen, and tips of the left and right wings, respectively [plane HBW_L and plane HBW_R in Fig. 2(b)]. The angle between the wings was used as a proxy for the wingbeat phase of the moth.

D. Acoustic signal processing

1. Transmit signal and system calibration

The transmit signal was a linearly modulated chirp with frequency sweeping from 60 to 20 kHz in 3 ms. This frequency range overlaps with the fundamental frequencies of the FM calls of many bat species (Jones, 1999) and the bandwidth provides adequate spatial sonar resolution after pulse compression (see below). The computer-generated chirp was tapered in the beginning and the last 10% of the signal by a

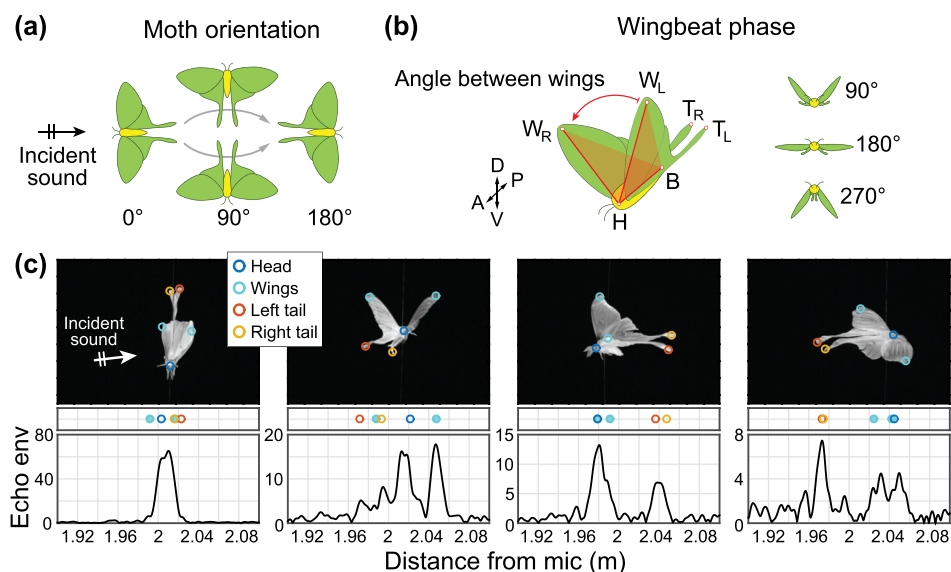


FIG. 2. (Color online) (a) Moth orientation with respect to the incident sound. (b) Locations of the various moth body parts reconstructed using video images and the definition of moth wingbeat phase. H: moth head; B: tip of abdomen; W_R and W_L : tips of the right and left wings, respectively; T_R and T_L : tips of the right and left tails, respectively. (c) Examples of video images and corresponding echo recordings. Top row: Video images captured at the moment of ensonification; Middle row: projected locations of moth body parts along the direction of incident sound; Bottom row: pulse-compressed echo envelopes (echo env) plotted on an arbitrary linear scale. The vertical axis limits on the bottom row vary due to the wide range of moth echo strengths. The sources of echo highlights are identified by comparing the highlights and projected locations of different body parts across the rows. Note the consistent amplitudes of tail echoes across all orientations and the strong echoes from the wings that mask the contributions from other moth body parts in the leftmost panel.

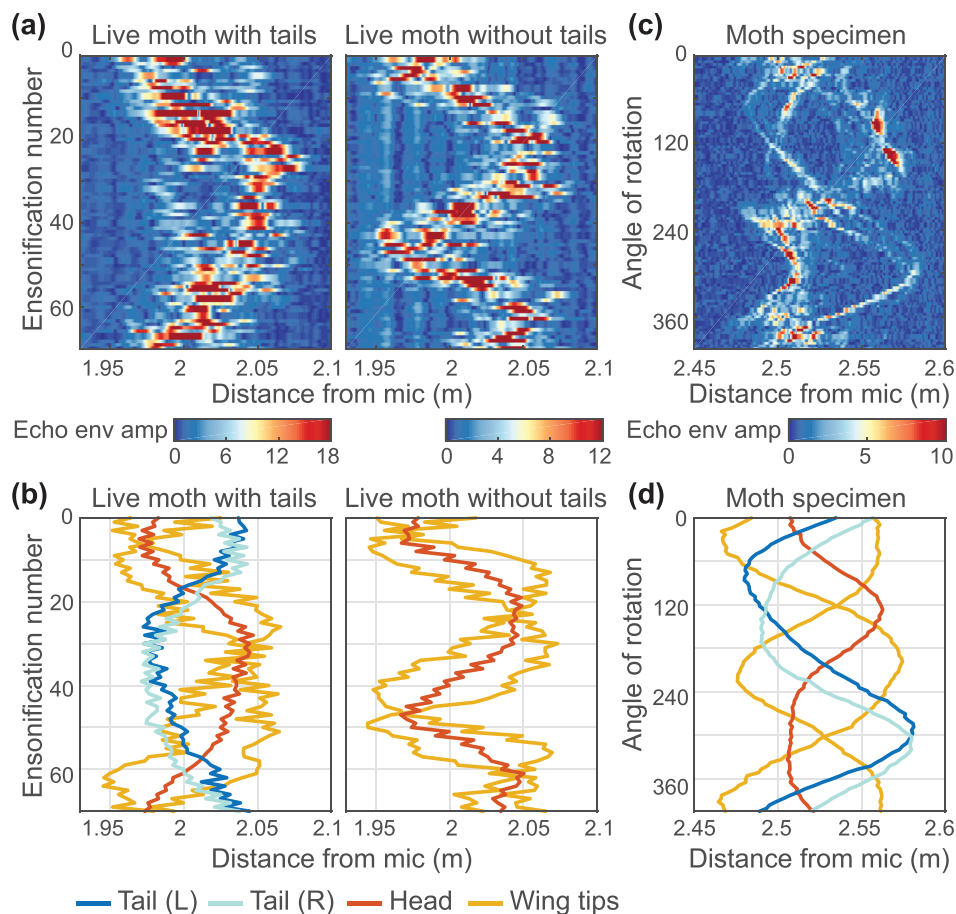


FIG. 3. (Color online) (a) and (b) Pulse-compressed echo envelopes (a) and the projected ranges of different body parts (b) from a live, fluttering luna moth with intact tails (left) and with the tails ablated (right). Echoes from the wings and moth body dominate the majority of sound reflections, as shown by the corresponding locations of the bright red stream of echoes in (a). Echoes from different body parts are easily distinguished due to the much more regular orientation changes of the tethered moth during measurements compared to in natural free-flying scenarios. The ensonification number represents the sequence in which echo data were collected at successive intervals of 50 ms (see Sec. II B). The orientation of live fluttering moths was not controlled. (c) and (d) Pulse-compressed echo envelopes (c) and projected ranges of different body parts (d) from a recently dead luna moth specimen. The moth body and the two tails dominate the echoes at all orientations. Echoes from the wings are minimal because they were parallel to the incident sound [see Fig. 1(b)]. Data are displayed according to the angle of rotation here because the orientation of the moth specimen was controlled.

tapered cosine (Harris, 1978). This transmit signal resulted in a usable band of 25–55 kHz when the frequency-dependent noise level is considered. The pulse-echo system was calibrated both before and after each experiment using the procedure described in Stanton *et al.* (1998), with the frequency-dependent atmospheric sound absorption compensated (ANSI, 1995).

2. Pulse compression

The received echo signal after each ensonification was compressed in time through cross-correlation with the received calibration signal to obtain the echo profile. This approach has been widely employed to analyze sonar echoes from live animals and other targets, both in the air and underwater (Au, 1993; Chu and Stanton, 1998; Moss and Zagaeski, 1994; Simmons and Chen, 1989). The improved temporal, and thus spatial, resolution through pulse compression was important in resolving moth features on a centimeter scale and segregating moth echoes from room reverberation. The pulse-compressed echoes can be treated as a weighted average across the frequency band of interest. Therefore, the peak

envelope amplitudes of pulse-compressed echo highlights were used as proxies for the relative contributions of echoes from different body parts of a moth (Stanton *et al.*, 1998).

3. Identification of echo sources within a fluttering moth

The sources of highlights in the pulse-compressed echo profile of a fluttering moth were identified by comparing the highlight locations and the projected ranges (i.e., distance from microphone) of different moth body parts along the direction of incident sound [Figs. 2(c) and 3]. Due to the geometry, echoes from different moth body parts were the most easily separable when the moth was oriented more parallel to the incident sound. The range-Doppler coupling resulted from the fluttering movement of the moth wings could lead to 1–3 mm of ranging ambiguity depending on the wingbeat phase (Levanon and Mozeson, 2004; Simmons and Stein, 1980). This ambiguity does not interfere with the identification of echo sources. In addition, echo highlights with normalized peak envelope amplitudes below 0.1 (level of the highest processing side-lobe) were excluded from the

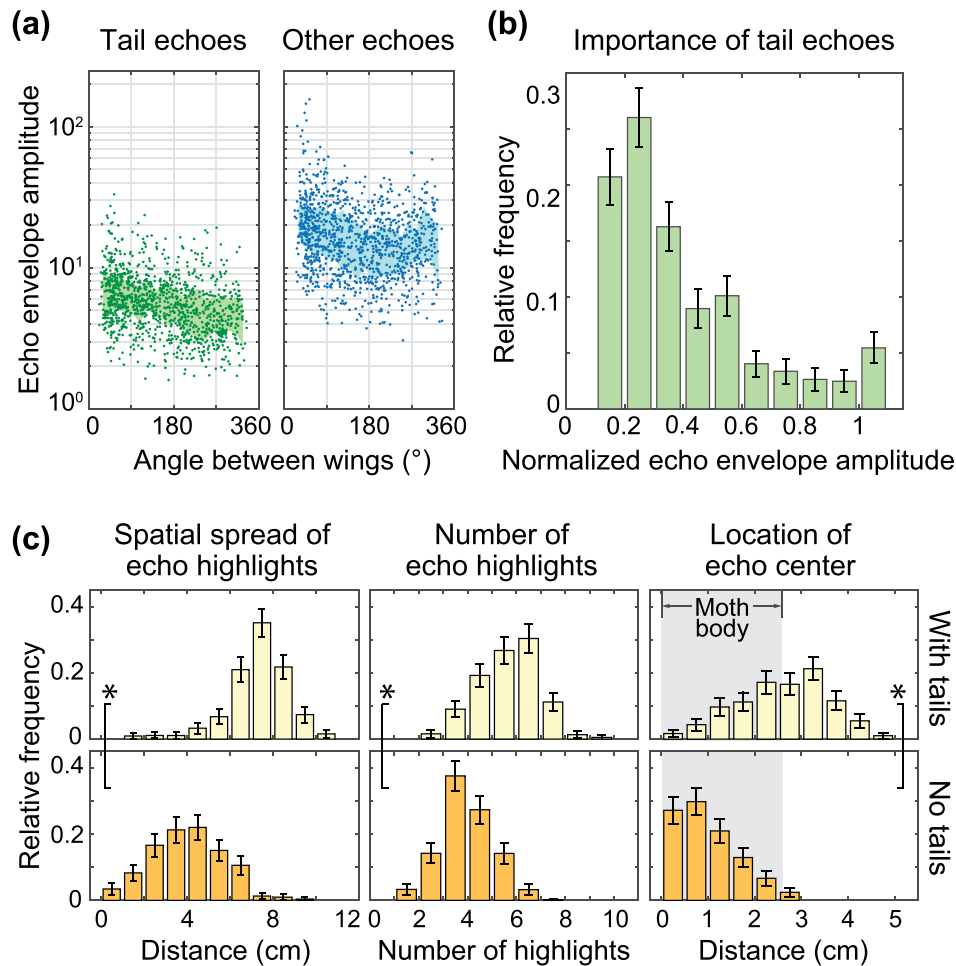


FIG. 4. (Color online) Echo-acoustic contributions of the luna moth tails. (a) Pulse-compressed envelope amplitude of echoes produced by the tails and other body parts (wings and body) of the moth. The shaded area represents the range from the 25% to 75% percentile. (b) Distribution of the normalized envelope amplitude of tail echoes. Samples with normalized echo envelope amplitude <0.1 are excluded to minimize contamination from side-lobe artifacts in pulse compression processing. The rightmost bar shows data with normalized tail echo amplitude = 1. Results in (a) and (b) show that the tail echoes do not dominate sound reflections from a fluttering luna moth. (c) Distributions of the spatial spread and number of echo highlights as well as the location of echo center across the wingbeat cycle for the same moth individual with intact tails and with the tails ablated (moth orientation $<30^\circ$ or $>150^\circ$). The tail echoes increase the complexity and spatial spread of the overall moth echoes by producing additional highlights (left two panels). They also displace the echo center caudally, causing potential sonar localization errors for foraging bats (rightmost panel). Error bars in the histograms represent standard deviations in bootstrap histogram estimation. All pairwise bootstrap comparisons are significant ($p < 0.01$).

analysis to avoid contamination of side-lobe artifact in pulse compression.

E. Modeling spatial localization of moth echoes by bats

The pulse-compressed echo time series was analyzed to model the sonar localization of fluttering moths by bats, with comparisons drawn between luna moths with intact and ablated tails. Specifically, the number and spatial spread of the echo highlights were used to quantify the spatial complexity in the moth echoes, and the center of the moth echo was used to model the error between the acoustically inferred and the actual moth locations [Fig. 4(c)]. The definitions of these various quantities are described below.

The spatial extent of moth echo (the “echo extent”) in the pulse-compressed profile was determined using a threshold-based method. The threshold was adaptively

determined by the background noise level in each experimental trial. Details of this method are discussed in the Appendix. The pulse-compressed echoes included within the echo extent were used to calculate the broadband moth target strength (TS) (Urlick, 1983), from which the average TS across the usable band was obtained. The TS averaging was conducted in the linear domain.

The location of the center of the moth echo extent (the “echo center”) measured from the moth head was used to model the potential error in the bat’s sonar tracking of moth based on echoes (see the Appendix for an example). Only data collected from moths oriented near parallel to the direction of incident sound ($<30^\circ$ or $>150^\circ$) were used for statistical analyses of the location of echo center to the moth head for moths with and without tails. This was used to infer the spatial acoustic information received by bats.

The number and spatial spread of echo highlights were used to quantify the spatial complexity in the echoes. Echo

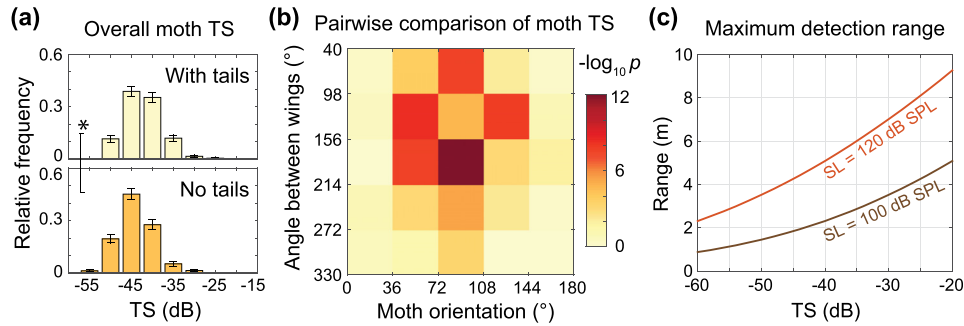


FIG. 5. (Color online) Target strength (TS) contribution of the tails and their influence on the detection range of moths by bats. (a) Distributions of moth TS from the same individual, measured with intact tails and with the tails ablated across all moth orientations and over the entire wingbeat cycle. The values shown here are TS averaged across the usable frequency band (Sec. II E). (b) Pairwise differences of TS from the same moth individual, measured with intact tails and with tails ablated across different moth orientations and wingbeat phases. Here, the negative logarithm of the p -values from the KS 2-sample test are used to summarize the results, with dark red indicating a larger difference. (c) Modeled maximum detection range of moth by bats using echolocation signals with two different source levels (SL). The overall mean TS increment induced by the tails (approximately 2 dB) is estimated to increase the bat's maximum target detection distance by 0.2–0.5 m.

highlights were identified by local peaks in the pulse-compressed echo profile with spacing larger than $50 \mu\text{s}$, chosen based on the ranging acuity of bats (Moss and Schnitzler, 1995; Simmons, 1973). As noted above, echo highlights with normalized echo envelope amplitudes smaller than 0.1 were excluded from the analysis to avoid contamination from side-lobe artifacts in pulse compression processing. The spatial spread of echo highlights was defined as the distance from the first to the last echo highlights.

F. Modeling detection of moth echoes by bats

The potential influence of the luna moth tails on the moth's risk of being detected by bats was investigated through use of the measured TS variation and the perceptual space model developed by Goerlitz *et al.* (2010) [Fig. 5(c)]. Following Goerlitz *et al.* (2010) and Surlykke *et al.* (1999), the bat's echo detection threshold was assumed to be 20 dB sound pressure level (SPL). Two echolocation source levels (100 and 120 dB SPL at 10 cm) were used in the model, as the source level emitted by foraging bats generally falls between these values. The sound transmission loss was determined by combining the spherical spreading loss and the air absorption at 40 kHz, which corresponds with the center frequency of the transmit signal used in this study.

G. Statistical analysis

A bootstrap procedure (Efron, 1982) was used to estimate the distribution of the normalized pulse-compressed echo envelope amplitude of the tails across all moth orientations and the wingbeat cycle [Fig. 4(b)]. The echo envelope amplitudes here are normalized with respect to the maximum echo envelope amplitude of each sonar return in order to quantify the relative scattering contribution of the tails (Chu and Stanton, 1998; Stanton *et al.*, 1998). The samples were divided into 25 groups according to the moth orientation and wingbeat phase (five bins spanning the measured wingbeat phases from 40° to 330° , and five bins spanning the measured moth orientations from 0° to 180°). Ten samples were drawn randomly from each of the 25 groups, resulting in a total of 250 samples for

each bootstrap repetition. One thousand repetitions were used to estimate the mean and standard deviation of the bootstrap histogram. This bootstrap procedure was also employed to estimate the overall distribution of average TS from the same luna moth individual with intact tails and with the tails ablated [Fig. 5(a)].

The same bootstrap procedure was used to estimate the distributions of the spatial spread and number of echo highlights, as well as the distance between the echo center and the moth head [Fig. 4(c)]. Here, the samples were divided into six combinations of moth orientation and wingbeat phase (three bins spanning the measured wingbeat phases from 60° to 330° , and two bins for the moth orientation: $<30^\circ$ or $>150^\circ$). A total of one thousand bootstrap repetitions were conducted, with twenty bootstrap samples drawn from each combination of moth orientation and wingbeat phase.

For all realizations, the distributions of bootstrap samples obtained from the same moth with and without tails were significantly different from each other [$p < 0.01$; Kolmogorov-Smirnov two-sample test (Conover, 1999) for the spatial spread of echo highlights, the location of echo center from the moth head, and the moth TS; Mann-Whitney U test (Conover, 1999) for the number of echo highlights].

III. RESULTS

The pulse-compressed echo envelope, or "echo profile," from a live, fluttering luna moth is characterized by a series of highly variable echo highlights, created by different body parts, including the wings, tails, and the moth body (thorax and abdomen) [Fig. 2(c)]. As the moth flutters, the number, amplitude, and location of echo highlights vary dramatically, owing to the changing orientation of each body part with respect to the incident sound. Echoes from the wings generally dominate the acoustic returns with great variability over consecutive ensonifications across the wingbeat cycle (Figs. 3 and 6 and Mm. 1). When ensonified nearly perpendicularly at the upstroke or downstroke extremes of the wingbeat cycle, the wing echoes

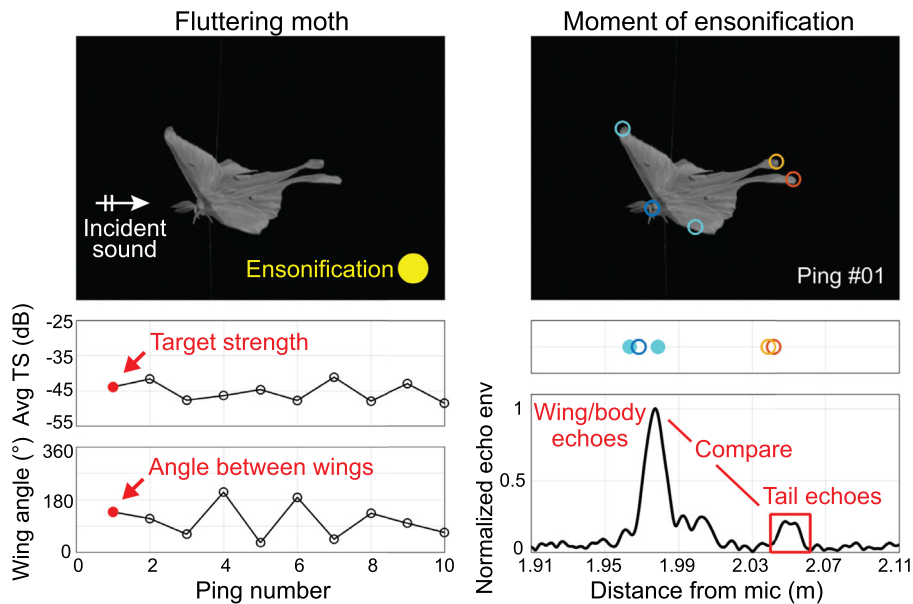


FIG. 6. (Color online) An annotated frame from the video [Mm. 1](#) showing corresponding pulse-compressed echo envelopes and video recordings from a fluttering luna moth. Echoes from the wings and body of the moth generally dominate the acoustic returns, which vary greatly over consecutive ensonifications across the wingbeat cycle. Note the echo envelopes shown here are normalized with respect to the maximum envelope amplitude of each sonar return.

are strong and can mask the scattering contributions from other body parts [e.g., Fig. 2(c), leftmost panel].

Mm. 1. Corresponding pulse-compressed echo envelopes and video recordings from a fluttering luna moth. Echoes from the wings and body of the moth generally dominate the acoustic returns, which vary greatly over consecutive ensonifications across the wingbeat cycle. File of type “mp4” (15.3 MB)

Echoes from the hindwing tails, on the other hand, are weaker but more consistent across all wingbeat phases and moth orientations [Figs. 2(c), 3(a), and 3(b)]. When the wings do not dominate reflections, echoes from the tails stand out and contribute to the overall echo profile [Fig. 2(c), the right two panels]. The broad scattering directionality of the tails can be explained by their twisted morphology, which creates a series of small surfaces facing different orientations along their length, returning echoes from a wide range of incident angles of sound (Morse and Ingard, 1987). This is in contrast to the much narrower scattering directionality of the large, planar surfaces of the wings.

Analysis of the echo profiles from live, fluttering luna moths is aided by measurements from a dead luna moth specimen that was tethered and ensonified across all angles of orientation in the lateral plane [Figs. 3(c) and 3(d)]. For the moth specimen, echoes from the twisted tails and the body are clearly identifiable across all angles, whereas echoes from the wings are negligible at this plane of ensonification. This is due to the wings’ parallel orientation relative to the direction of incident wave, which results in minimal surface for sound reflection [Fig. 1(b)].

In contrast to earlier speculation that luna moth tails return echoes that are comparable in strength to those from the wings (Barber *et al.*, 2015; Weeks, 1903), echoes from the tails of fluttering moths are in fact much weaker than

those from the wings or moth body across most of the wingbeat cycle [Fig. 4(a)]. To understand the *relative* scattering contribution of different body parts, the echo profiles are normalized with respect to the maximum envelope amplitude of each sonar return (Chu and Stanton, 1998; Stanton *et al.*, 1998). The relative contribution of the tails varies considerably from one sound reflection to the next, across all angles of moth orientation and cycle of the wingbeat (Fig. 6 and [Mm. 1](#)). The majority ($72.0 \pm 2.7\%$) of the tail echoes are weak compared to those from the wings/body (normalized echo envelope amplitude < 0.5), and only $7.9 \pm 1.7\%$ of the samples show strong echo contribution from the tails [normalized echo envelope amplitude > 0.9 ; see Fig. 4(b)]. Therefore, the tails rarely produce echoes of competing amplitudes with those from the vital wings and body of the moth. In addition, the tails only incrementally increase the average moth TS at specific moth orientations and postures, and the overall TS increment would not substantially affect the bat’s detection range of the moth (Fig. 5). This is consistent with previous suggestions that the anti-predator function of the tails only manifests at the final stage of prey capture (Barber *et al.*, 2015).

The echo profiles of luna moths with intact hindwing tails and with the tails ablated are also compared to characterize the potential influence of tail echoes on prey localization by bats. The tails increase the complexity and spatial spread of the overall moth echoes by producing additional highlights that could confuse the bat predator [Fig. 4(c), left two panels] (Simmons *et al.*, 1990). The scattering contribution of the tails also displaces the center of the echo profile (echo center) away from the moth thorax [Fig. 4(c), rightmost panel]. Here, the echo center is used to model the bat’s estimate of the average prey location through echolocation. As the thorax houses vital organs of the moth, the further away the echo center is from the thorax, the greater the probability the bat’s attack would be directed away from moth vital body parts. The

percentage of samples with the echo center falling beyond the tip of the abdomen—and therefore more likely that the bat’s attack would be directed away from the thorax—is significantly higher for moths with intact tails compared to those without tails ($53.0 \pm 2.4\%$ and $2.4 \pm 1.4\%$, respectively). The difference between these two values is comparable to the improved survival rate of moths with intact tails (46.8%) reported in Barber *et al.* (2015).

IV. DISCUSSION

Our echo-acoustic measurements indicate that the hindwing tails cannot act as consistent and strong competing echo sources to lure bat attacks toward non-vital body parts of the moth. Instead, with their distinctive twisted morphology, the tails produce weak but persistent echoes across all angles of ensonification. These tail echoes do not dominate the sound reflection from fluttering luna moths over most of the wingbeat cycle, but instead introduce complexity in the echo profile [Figs. 2(c), 3(a), 3(b), and 4(c)]. These findings suggest that the false target hypothesis (Barber *et al.*, 2015; Weeks, 1903) should be revised to more accurately convey the echo-acoustic contribution of the twisted tails.

If the elongated hindwing tails do not produce competing echoes to distract the bat’s attention away from the thorax, what may explain the observed higher rate of survival under bat predation by moths with intact tails? To address this question, we consider the bat’s sonar-based foraging behavior and prey localization accuracy. During the course of prey pursuit, a bat faces the challenge of devising its plan of attack by integrating information from discrete “acoustic snapshots” of the prey obtained through intermittent biosonar emissions (Moss and Surlykke, 2001; Moss *et al.*, 2011). The resulting sonar images are formed based on perceived echo delays, with a ranging accuracy of $50 \mu\text{s}$ (approximately 1.7 cm), which is susceptible to amplitude-latency trading of neural responses, where weaker echoes are perceived at longer delays (Bates *et al.*, 2011; Burkard and Moss, 1994; Simmons *et al.*, 1990).

Is it possible that the tail echoes function to confuse the bat’s sonar tracking of prey? In the face of complex echoes from fluttering moths, the bat may direct its aim of attack toward individual echo highlights that are vital body parts for the moth, such as its wings that power flight and its thorax and abdomen that harbor essential organs. However, the bat’s strategy could fail for intercepting moths with twisted hindwing tails whose echoes contain more highlights over a wider spread in space [Fig. 4(c), left two panels]. The bat may mitigate this spatial uncertainty associated with highly variable echoes by aiming its attack toward the center of target echo streams. This approach would be effective for bats capturing moths without tails, whose vital thorax co-locates with its echo center, but could fail for bats pursuing moths with intact hindwing tails, as the tails serve to shift the echo center beyond the moths’ abdomen with a high probability [Fig. 4(c), rightmost panel]. As such, the twisted hindwing tails of luna moths are efficient morphological adaptations

that increase complexity in the echoes to disrupt accurate sonar tracking of bat predators.

The physics-based approach of echo analysis employed here beckons further study of different saturniid moths that show distinct hindwing tail morphologies. For example, moths of the genera *Argema* and *Eudaemonia* possess exceptionally elongated and slim tails with substantially enlarged and twisted knob-like tips (D’Abrera, 1998). Compared to the shorter tails of luna moths, tails with these morphological features would induce strong echoes at larger distances away from the moth body. The wide range of species differences in hindwing tail morphology provides a valuable comparative basis for future studies to more thoroughly investigate the contribution of moth tails to bat sonar target tracking and prey capture.

Building on past studies of insect echoes (Emde and Schnitzler, 1990; Goerlitz *et al.*, 2010; Moss and Zagaeski, 1994; Simmons and Chen, 1989; Surlykke *et al.*, 1999), the data and analyses presented in this study address the connections among moth morphology, echo characteristics, and their potential influence on the bat’s prey capture performance. The results suggest that the echoes from luna moth tails, although weaker than echoes from the wings and the moth body, may induce erroneous target localization and challenge the bat’s sonar tracking behavior at the final stage of prey capture. Our empirical study thus provides a different interpretation of the behavioral observation that the twisted tails increase the survival rates of luna moths under the attack by naive bats (Barber *et al.*, 2015).

A variety of other factors may, in fact, have contributed to the reported differences in survival rates of luna moths with intact or ablated tails. For example, the tails may induce more erratic flight patterns and act in conjunction with acoustic scattering effects to facilitate the disruption of sonar target tracking by bats. Tail ablation may have interfered with the moths’ sensing and flight kinematics, as well as escape mechanisms, making them more vulnerable to bat predation. Experimental and computational analyses of moth flight aerodynamics and sensory feedback are required to investigate these possibilities in future studies. More broadly, our findings illustrate how physics-based approaches to understand the dynamics of natural stimuli can shed light on sensory information underlying predator-prey interactions.

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APPENDIX

A threshold-based method was developed to adaptively determine the extent of the moth echo according to the background noise level in each experimental trial [Fig. 7(a)]. A Rayleigh distribution was first fit to the distribution of the pulse-compressed echo envelope amplitude within a 200 μ s background section immediately before the approximate range of moth echo arrivals for each experimental trial. The amplitude at which the cumulative density function of the background envelope amplitude reaches 99.9% was used as the threshold. The echo extent was defined between the start and end locations of the echo envelope above the threshold. To ensure accurate estimation, coherent room reverberation was obtained by averaging all echo time series within the same trial and subtracted from each echo prior to the above operation. The subtraction of room reverberation was not performed elsewhere in this study to avoid contamination of echo data. The above procedure was performed semi-automatically with supervised correction of erroneous detection.

The echo center is determined by the midpoint of the moth echo extent. The location of the echo center measured from the moth head was used as a proxy to quantify the potential error in the bat's sonar tracking of moth based on echoes [Fig. 4(c), rightmost panel, and Sec. III]. Examples of the locations of both the echo center and moth head are shown in [Fig. 7(b)].

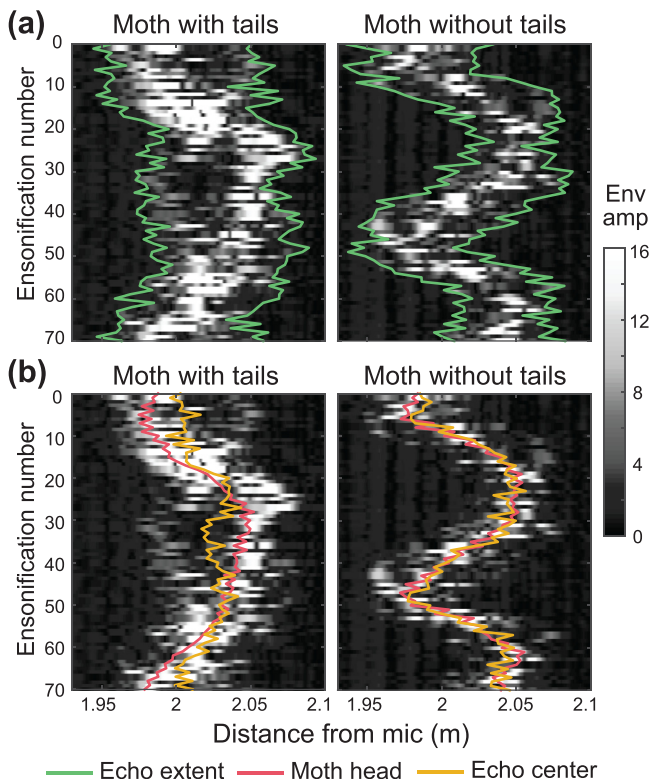


FIG. 7. (Color online) Spatial analysis of moth echoes. (a) The start and end positions of the echo extent and (b) the locations of the echo center and moth head for the same luna moth individual, with intact tails (left) and with the tails ablated (right). The underlying echo profiles are identical to those shown in Figs. 3(a) and 3(b).

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