

Volume 93

An NRC Research
Press Journal

Une revue de
NRC Research
Press

2015

www.nrcresearchpress.com

Canadian Journal of
Zoology

Revue canadienne de
zoologie



In cooperation with the
Canadian Society of Zoologists



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Research Press

Negligible energetic cost of sonar jamming in a bat–moth interaction

A.J. Corcoran and H.A. Woods

Abstract: Energetic cost can constrain how frequently animals exhibit behaviors. The energetic cost of acoustic signaling for communication has been the subject of numerous studies; however, the cost of acoustic signaling for predator defense has not been addressed. We studied the energetic cost and efficiency of sound production for the clicks produced by the moth *Bertholdia trigona* (Grote, 1879) (Grote's bertholdia) to jam the sonar of predatory bats. This moth is an excellent model species because of its extraordinary ability to produce sound—it clicks at the highest known rate of any moth, up to 4500 clicks·s⁻¹. We measured the metabolic cost of clicking, resting, and flying from moths suspended in a respirometry chamber. Clicking was provoked by playing back an echolocation attack sequence. The cost of sound production for *B. trigona* was low (66% of resting metabolic rate) and the acoustic efficiency, or the percentage of metabolic power that is converted into sound, was moderately high (0.30% ± 0.15%) compared with other species. We discuss mechanisms that allow *B. trigona* to achieve their extraordinary clicking rates and high acoustic efficiency. Clicking for jamming bat sonar incurs negligible energetic cost to moths despite being the most effective known anti-bat defense. These results have implications for both the ecology of predator–prey interactions and the evolution of jamming signals.

Key words: energetics, bioacoustics, predator–prey, sonar jamming, sound production, *Bertholdia trigona*, Grote's bertholdia.

Résumé : Les coûts énergétiques peuvent restreindre la fréquence des comportements adoptés par les animaux. Si les coûts énergétiques de la production de signaux acoustiques pour la communication ont fait l'objet de nombreuses études, les coûts de la signalisation acoustique comme moyen de défense contre les prédateurs n'ont pas été examinés. Nous avons étudié les coûts énergétiques et l'efficacité de la production de sons pour des clics produits par le papillon nocturne *Bertholdia trigona* (Grote, 1879) pour brouiller le sonar de chauves-souris prédatrices. Ce papillon est une excellente espèce modèle en raison de son extraordinaire capacité de produire des sons—il produit des clics à une fréquence inégalée chez les papillons nocturnes allant jusqu'à 4500 clics·s⁻¹. Nous avons mesuré le coût métabolique de la production de clics, du repos et du vol chez des papillons suspendus dans une chambre respirométrique. Les clics étaient provoqués par la diffusion d'une séquence d'attaque d'écholocation. Les coûts de la production de sons pour *Bertholdia trigona* étaient faibles (66 % de l'énergie métabolique au repos) et l'efficacité acoustique, ou le pourcentage de la puissance métabolique convertie en son, était modérément élevée (0,30 % ± 0,15 %) comparativement à d'autres espèces. Nous discutons des mécanismes qui permettent à *B. trigona* d'atteindre ses extraordinaires fréquences de clics et sa grande efficacité acoustique. La production de clics pour brouiller le sonar de chauve-souris entraîne des coûts énergétiques négligeables pour les papillons nocturnes, même s'il s'agit du mécanisme de défense connu le plus efficace contre les chauves-souris. Ces résultats ont des répercussions en ce qui concerne tant l'écologie des interactions prédateur–proie que l'évolution du brouillage de signaux. [Traduit par la Rédaction]

Mots-clés : énergétique, bioacoustique, prédateur–proie, brouillage de sonar, production de sons, *Bertholdia trigona*.

Introduction

The energetic cost of acoustic signaling can be sufficiently high to constrain sound-producing behaviors and in some cases can even exceed that of locomotion (Prestwich 1994; Stoddard and Salazar 2011). Costly acoustic signals frequently occur when the interests of the signaler and receiver diverge, or when signals are sent over long distances or at high rates (Stoddard and Salazar 2011). The energetics of signaling to potential mates has been studied for numerous organisms (reviewed by Prestwich 1994; Stoddard and Salazar 2011). By contrast, the energetics of antipredator signaling has not been addressed. Tiger moths (Lepidoptera, Arctiinae) defend themselves from bats by producing bursts of ultrasonic clicks from paired metathoracic tymbal organs. Depending on the rate at which clicks are produced and whether or not the moth is toxic, moth clicks can warn bats of toxicity, mimic clicks of toxic moths, or jam

bat echolocation (reviewed by Conner and Corcoran 2012). The palatable tiger moth *Bertholdia trigona* (Grote, 1879) (Grote's bertholdia) produces clicks at the highest known rate among moths (up to 4500 clicks·s⁻¹) to jam bat sonar (Corcoran et al. 2009). This makes *B. trigona* (the focal species here) an excellent model for the study of sound production.

An animal can decrease the total cost of signaling either by producing sound less often or by producing it more efficiently. Acoustic efficiency is the amount of acoustic power generated per unit of net metabolic power expended (Prestwich 1994). Animals produce sound within a wide range of acoustic efficiencies (0.008%–6%; Prestwich 1994; Reinhold et al. 1998). Acoustic efficiency is strongly affected by two factors: first, how the energy produced by muscles is transduced into vibrations of the radiating structures, and second, how well the acoustic resistance of the radiating structures matches that of the medium (Bennet-Clark

Received 25 August 2014. Accepted 15 December 2014.

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1998). For monopole radiators such as the tymbals of tiger moths, acoustic resistance is matched between radiator and medium when the diameter of the source is one-third of the sound's wavelength (Prestwich 1994; Bennet-Clark 1998).

The high clicking rates of jamming moths, combined with competing interests of predator and prey, led us to hypothesize that the instantaneous energetic cost of jamming clicks should be relatively high. However, because the moths use the defense sparingly, clicking only in the last few hundred milliseconds of an attack (Corcoran et al. 2013), we predicted that clicking cost would be an insubstantial portion of the animal's energy budget. We also predicted that the *B. trigona* sound production mechanism must be highly efficient to attain the unusually high clicking rates used for jamming bats.

We used respirometry and acoustic analysis to examine the energetic cost and acoustic efficiency of sonar-jamming moth clicks in *B. trigona*. Our results provide the first energetic assessment of antipredator signaling in a group of over 11 000 species that click for varied purposes. We found that the instantaneous energetic cost of *B. trigona* clicking is low and effectively negligible to the animal's energy budget. This is achieved in part by an efficient sound production mechanism.

Materials and methods

Animal care

Bertholdia trigona moths were collected at ultraviolet lights and tested at the Southwestern Research Station, near Portal, Arizona, USA, during July 2010. Moths were held at ambient temperature and normal daylight cycles for up to 36 h before experimentation.

Overview

Moths were suspended in a 220 mL glass respirometry chamber by an insect pin affixed to the moth's mesoscutum allowing for full range of wing motion. The moth's behavior (resting, agitation, shivering, or flying) was noted and time-synced with respirometry data. After the moth rested or flew for approximately 30 s, a 2.1 s prerecorded attack sequence of the big brown bat (*Eptesicus fuscus* (Palisot de Beauvois, 1796)) was broadcast to provoke moth clicking (see Corcoran et al. 2010). A custom, miniature, "ear-bud" speaker was used to broadcast bat calls that were recorded at a 250 kHz sample rate. The speaker was placed 2 cm behind the moth in the chamber. Sounds were broadcast at 100 dB SPL at the moth's position (re. 2×10^{-5} μ Pa) and calibrated with a Brüel and Kjær (B&K) 2610 measuring amplifier with a 1/4-inch B&K microphone (grid off). The moth's acoustic response was recorded using a 2 mm diameter microphone (Knowles Acoustics FG-3329) connected to an AR100 ultrasound receiver (Binary Acoustics Technology, Tucson, Arizona, USA) sampling at 250 kHz. The microphone was placed 2 cm behind the moth.

Respirometry

Moth metabolic rates were estimated as rates of CO₂ emission using flow-through respirometry (Lighton 2008). CO₂ was measured using a Licor LI-7000 CO₂/H₂O analyzer (Licor, Lincoln, Nebraska, USA) calibrated with pure N₂ and 100 ppm CO₂ in N₂ (Norco). Dry, CO₂-free air (1 standard L·min⁻¹) was first directed through the reference cell and then through a water-jacked flask containing 20 °C water to humidify it to 65%–70% relative humidity. The excurrent stream was directed through the respirometry chamber then into the measurement side of the analyzer. Temperature in the respirometry chamber was measured with type T thermocouple connected to a TC-1000 m (Sable Systems, Las Vegas, Nevada, USA). Voltage outputs from the thermocouple meter and gas analyzer were sent to an A/D converter (UI2; Sable Systems) and from there to a computer running Expedata software version 1.1.9 (Sable Systems). The chamber was opened briefly, the moth introduced, and the chamber closed. Chamber readings stabilized in <1.5 min and measurement periods lasted 5–30 min·moth⁻¹.

Before and after each trial we took baseline measurements, which were used to correct drift.

Windows of data corresponding to each moth activity described above were extracted and, together with known flow rates (1 standard L·min⁻¹), were used to estimate emission rates of CO₂. Traces were corrected for dilution by water vapor. Because this study focused on metabolic signals from brief events (clicking), we evaluated how a point release of CO₂ by the moth showed up in the gas analyzer. We therefore injected CO₂ just upstream from the empty chamber and measured the shape of the pulse as it passed through the Licor. Pulses were detectable starting 4 s after injection and peaked at 7 s. Subsequent washout was exponential, falling to within 5% of the baseline value by 50 s after injection. These measurements indicate that the flow-through system had a fast response time and that the respirometry chamber acted as a continuously stirred tank reactor. We therefore used Bartholomew's transformation to calculate instantaneous rates of CO₂ emission (Bartholomew et al. 1981). This approach uses instantaneous rates of change in measured levels of CO₂, together with the known washout kinetics of the respirometry chamber, to estimate (moment to moment) what the instantaneous rate of CO₂ emission must be. We use these instantaneous rates in all subsequent metabolic figures and analyses.

Acoustics

We used custom scripts in Matlab R2012 (The MathWorks, Inc., Natick, Massachusetts, USA) to measure acoustic parameters of moth clicks produced in response to playbacks for moths at rest and moths in flight. We measured the total duration of clicking bouts and the number of modulation cycles produced per unit time of clicking.

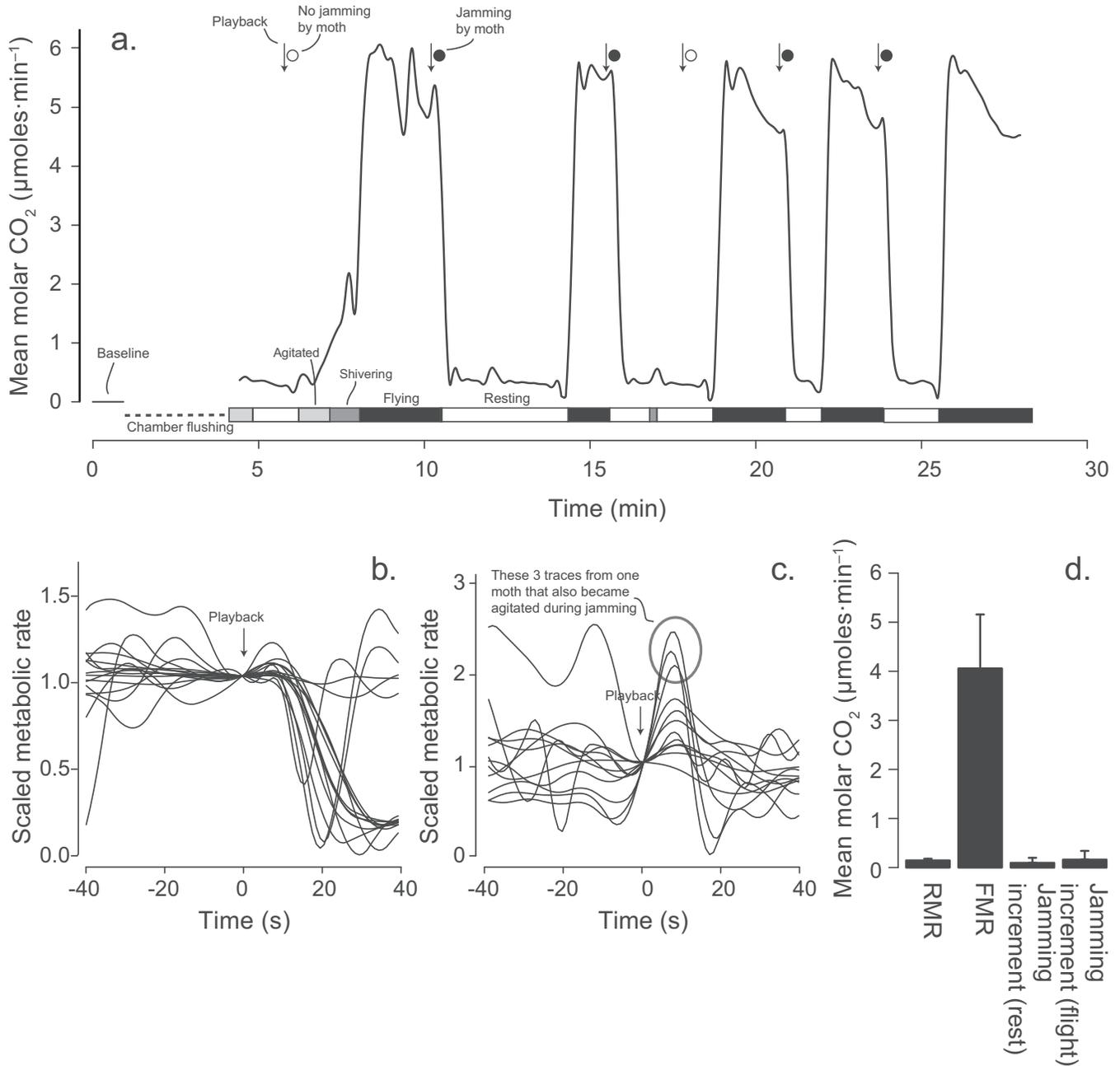
To determine sound production efficiency (acoustic power divided by net metabolic power; Prestwich 1994), we measured sound pressure levels at 45° intervals over the right half of a 10 cm radius sphere surrounding seven moths suspended with wings folded dorsally and clamped in a hemostat in a sound recording room (5 m × 12 m × 3.5 m). Sound pressure levels were measured with the B&K microphone and measuring amplifier. The sequence of recording locations was randomized for each moth. The left hemisphere of sound directionality was assumed symmetrical to the right. Root mean square (RMS) sound pressure levels (dB re. 2×10^{-5} μ Pa) were used to determine averaged sound amplitudes. The measuring amplifier was set to "fast" RMS averaging with a 22.4 Hz high-pass filter. We applied a correction factor to account for click durations that did not meet the amplifier's averaging time (Prestwich et al. 1989). We used an Avisoft USGH 416H recording unit (Avisoft Bioacoustics, Berlin, Germany) sampling at 300 kHz with an Avisoft CM16/CPMA ultrasound microphone to record moth clicks for duration measurements. The Avisoft microphone was placed 20 cm to the lateral side of the moth. Moths were induced to click using tactile stimulation of the head with a 2 mm diameter blunt instrument, with care taken to minimize impact on the moth sound field and body axis. Three recordings per location were made at 10–15 s intervals and averaged for each moth. Efficiency calculations were made as previously described using an intermediate respiratory quotient of 0.8 (Prestwich et al. 1989).

Statistical analysis

Metabolic data were processed using scripts in R (version 2.15.0) and data were analyzed using linear mixed-effects (LME) models, which can account for the repeated measures made on individual moths (R Development Core Team 2012; Pinheiro et al. 2013).

Acoustic data were found to have non-normal distributions based on inspections of histogram plots and Kolmogorov–Smirnov tests. Distributions of acoustic measurements for the flight and rest conditions were compared using Wilcoxon's rank-sum tests.

Fig. 1. Instantaneous rates of CO₂ emission by the moth *Bertholdia trigona* at rest, during flight, and during sonar jamming (clicking). Instantaneous rates were calculated from measured CO₂ values using Bartholomew's transformation (Bartholomew et al. 1981). (a) A typical trace of CO₂ emission by a tethered moth. Rates of emission were lowest when the moth was resting, started to rise when it became agitated, and rose to high and relatively stable levels in flight. At various points, we broadcast bat calls (indicated by vertical arrows) and recorded whether or not the moth emitted a jamming signal (solid circles if it did, open circles if not). This moth clicked only when it was flying. Every time it did so, it also stopped flying and its CO₂ emission dropped precipitously. (b) Metabolic traces just before and after jamming when moths were flying. Each trace was scaled to the measured metabolic rate at the moment of jamming (15 traces from seven moths; not all moths responded to bat calls when they were flying, thus, only instances in which a playback was followed by jamming were included in this analysis). Most moths sustained low metabolic rates after jamming because they stopped flying for several minutes. Three moths, however, stopped flying just for a few seconds then resumed flying. (c) Metabolic traces just before and after jamming when moths were at rest (12 traces from five of the moths). (d) Metabolic summary. The first two bars indicate mean (+SD) rates of CO₂ emission at rest and during flight (N = 12 moths). The third and fourth bars show the positive increments in mean (+SD) rates of CO₂ emission arising from jamming when at rest (N = 5 moths) and during flight (N = 7 moths), respectively. RMR, resting metabolic rate; FMR, flight metabolic rate.



Results

Metabolic rate depended strongly on activity (Figs. 1a, 1d). Resting metabolic rates (RMR) were low ($0.146 \pm 0.034 \mu\text{mol CO}_2 \cdot \text{min}^{-1}$), whereas flight metabolic rates (FMR) were much higher ($4.057 \pm 1.100 \mu\text{mol CO}_2 \cdot \text{min}^{-1}$), giving an aerobic scope (ratio of activity to RMR) of approximately 28. The difference between RMR and FMR was significant (LME, $t_{132} = -18.6$, $P < 0.0001$). The intermediate activities of agitating and shivering led to rapidly rising metabolic rates between RMR and FMR (Fig. 1a).

We played bat calls to moths during both flight and rest. The duration of clicking bouts for moths in flight (median = 741 ms, quartile range = 422–953 ms, $N = 18$) and resting moths (median = 556 ms, quartile range = 499–664 ms, $N = 12$) was not significantly different (Wilcoxon's rank-sum test, $z = -0.95$, $P = 0.34$). However, the number of clicking modulation cycles produced per second for moths in flight (median = 75.5 modulation cycles $\cdot \text{s}^{-1}$, quartile range = 70–79.5 modulation cycles $\cdot \text{s}^{-1}$) and resting moths (median = 68 modulation cycles $\cdot \text{s}^{-1}$, quartile range = 60–73 modulation cycles $\cdot \text{s}^{-1}$) was significantly different (Wilcoxon's rank-sum test, $z = -2.2$, $P = 0.027$).

In most cases (15 of 18), flying moths emitted ultrasonic clicks and simultaneously stopped flying (see Fig. 1a), which may be part of the moth's evasive diving behavior (Corcoran and Conner 2012). As a consequence, postclicking metabolic rates declined steeply toward RMR. Any CO_2 signal associated with clicking would therefore appear rapidly just after playback. The traces for flying (Fig. 1b) and resting (Fig. 1c) moths showed detectably higher rates of CO_2 emission around 7 s after playback (the transfer time between CO_2 emission and its peak in the CO_2 detector). For moths in flight, postclicking metabolic rates rose by $4.5\% \pm 1.5\%$ (mean \pm SE), which was statistically significant and corresponds to an absolute increment of $0.162 \pm 0.178 \mu\text{mol CO}_2 \cdot \text{min}^{-1}$ (LME, $t_{19} = 2.9$, $P = 0.018$), or 122% of RMR. For moths at rest, postclicking rates rose by $45\% \pm 17\%$ (mean \pm SE), which was marginally significant and corresponds to an absolute increment of $0.096 \pm 0.103 \mu\text{mol CO}_2 \cdot \text{min}^{-1}$ (LME, $t_{17} = 2.06$, $P = 0.078$), or 66% of RMR.

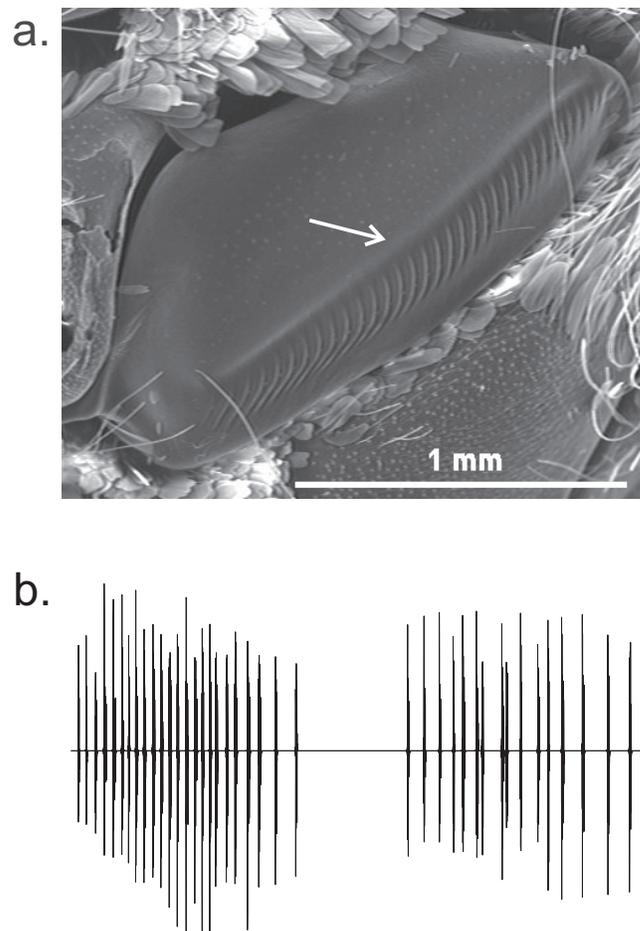
Moth clicks had RMS sound pressure level of 74.0 ± 1.9 dB at 10 cm ($N = 7$) when averaged over a three-dimensional sphere surrounding the moths. This value converts to an acoustic intensity of $0.0251 \pm 0.0138 \text{ mW} \cdot \text{m}^{-2}$. We divided this result by the surface area of a sphere with a 10 cm radius (0.126 m^2) to calculate an acoustic power output of $0.003 \pm 0.002 \text{ mW}$. This value was calculated from moths at rest, therefore we used the net metabolic cost of moths clicking at rest ($0.096 \pm 1.122 \mu\text{mol CO}_2 \cdot \text{min}^{-1}$) to calculate metabolic power input. Molar CO_2 production was converted to volumetric CO_2 production ($2.5 \times 10^{-6} \pm 2.6 \times 10^{-6} \text{ L} \cdot \text{min}^{-1}$) using the ideal gas law with a temperature of 22°C and pressure of 0.93 atm (1 standard atm = 101.325 kPa). This value was converted to volume of O_2 consumption using an intermediate respiratory quotient of 0.8 (Prestwich et al. 1989). Oxygen consumption was converted to power input of $1.05 \pm 1.12 \text{ mW}$ using the conversion $20.08 \text{ J} \cdot \text{mL O}_2 \text{ consumed}$ (Schmidt-Nielsen 1990). The metabolic power input was divided by the acoustic power output to give an acoustic efficiency of $0.30\% \pm 0.15\%$.

The diameter of the *B. trigona* tymbal, as measured from the scanning electron micrograph in Fig. 2a, is 1.7 mm. Based on a peak frequency of 51.2 kHz (Corcoran et al. 2009), the ratio of the size of the *B. trigona* tymbal to the wavelength of the emitted sound is 0.26, which is close to the ideal value of 0.33 for matching acoustic resistance between emitter and medium.

Discussion

Here we report the first measurement of the energetic cost of antipredator acoustic signaling. Compared with the cost of flight, the

Fig. 2. Sound production of the moth *Bertholdia trigona*. (a) Scanning electron micrograph of the tymbal organ. Arrow indicates striae. (b) Waveform of a single contraction and relaxation of the tymbal organ from one muscle contraction. For details see the text and the Supplementary Video S1,¹ which shows slowed-down (30 \times and 100 \times) audio and video of the *B. trigona* tymbal in action. From Corcoran et al. (2009), reproduced with permission of Science, vol. 325, issue 5938, p. 326, © 2009 American Association for the Advancement of Science.



cost of clicking was low for moths at rest and in flight (Figs. 1a–1d). Based on our measurement of the cost of clicking at rest, which is more comparable with conditions in other studies, *B. trigona* has one of the lowest relative costs of acoustic signaling (66% of RMR) and one of the higher acoustic efficiencies (0.3%) of those animals measured (Prestwich 1994; Stoddard and Salazar 2011). Acoustic efficiency of the *B. trigona* tymbal is slightly lower than that of the bladder cicada (*Cystosoma saundersii* Westwood, 1851) (0.82% acoustic efficiency); however, it is much higher than that of the lesser wax moth (*Achroia grisella* (Fabricius, 1794)), which has a remarkably low acoustic efficiency of 0.008% (MacNally and Young 1980; Reinhold et al. 1998).

Because flying moths stopped flying as they began clicking, it is possible that our net measurement of clicking metabolic cost is an underestimate. We believe this is unlikely for three reasons: (1) moths in flight clicked for the same duration as moths at rest and at only a slightly higher rate (median: 68 vs. 75 modulation cycles $\cdot \text{s}^{-1}$); (2) the few moths that did not stop flying while clicking (relatively flat traces from 0 to 40 s in Fig. 1b) had similar peaks in

¹Supplementary Video S1 is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2014-0231>.

metabolic traces as those that stopped flight; and (3) the measurements of clicking metabolic cost for moths in flight and at rest were similar (Fig. 1d).

Bertholdia trigona click only after being targeted by a bat (Corcoran et al. 2013) and then only for a fraction of a second (Corcoran et al. 2009; Corcoran and Conner 2012). It is unknown how frequently moths encounter bats in nature, but even if they did so once every 10 s in flight, clicking would account for only 0.16% of the animal's energy budget, an effectively negligible contribution. This result supports our prediction that clicking is a small component of the animal's energy budget because of its infrequent use. The low instantaneous and total costs of clicking indicates that energetics does not constrain the use of *B. trigona*'s jamming defense. Instead, moths use acoustic cues of bat echolocation intensity and pulse rate to initiate clicking as soon as they have been targeted by a bat (Corcoran et al. 2013).

These results contradicted our prediction that instantaneous clicking costs would be high. *Bertholdia trigona* produces up to 4500 clicks·s⁻¹, the highest rate measured for a tiger moth, of which there are over 11 000 species (Kitching and Rawlins 1998; Conner and Corcoran 2012). This extraordinary clicking rate and the moderate to high acoustic efficiency are achieved in part by four mechanisms: (1) paired tymbal organs operating in asymmetry; (2) elastic recoil allowing half of the clicks to be produced as the tymbal buckles inwards from muscle-produced tension and half as the structure returns to its original form through elastic recoil; (3) elaborate striations on the tymbal surface that allow each deformation of the tymbal to produce 20–30 clicks (Figs. 2a, 2b; Supplementary Video 1¹); and (4) a close matching of acoustic resistance of the tymbal to that of air, as evidenced by the tymbal diameter-to-wavelength ratio of 0.26, which is close to the theoretical optimum of 0.33. Other animals employ similar mechanisms to enhance sound production. For example, cicada tymbals have the same general features as those described above for *B. trigona* with the exception that they produce little sound as they recoil to their original position (Young and Bennet-Clark 1995). The feature that stands out on the *B. trigona* tymbal is the large number of striations (Fig. 2a), a feature that appears to have evolved to enable the high clicking rates required for jamming bat sonar (Corcoran et al. 2010).

Energetic cost typically scales with sound production rate (Prestwich 1994). Therefore, our results suggest that clicking in tiger moths has little energetic consequence, whether used for sonar jamming, acoustic aposematism, acoustic mimicry, or courtship (Conner 1999; Conner and Corcoran 2012). Clicking for sonar jamming may have evolved from clicking for acoustic aposematism, which requires only a simple sound-producing organ (Hristov and Conner 2005). If so, the refinement of the sound production mechanism for higher clicking rates came with little energetic cost. Despite being the most effective known defense against attacking bats (Corcoran and Conner 2012), energetically, jamming bat echolocation is nearly free.

Acknowledgements

The staff of the Southwestern Research Station provided logistical support. W. Conner wrote useful comments on a previous version of the manuscript and N. Hristov and the Center for Design Innovation helped film moth tymbals. Funding was provided by Wake Forest University (A.J.C.), the National Science Foundation (IOS 0844916 to H.A.W.), and the National Institute of Deafness and Communicative Disorders of the National Institutes of Health (UMD T32 DC-00046).

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