THE EVOLUTION OF ANTI-BAT SENSORY ILLUSIONS IN MOTHS

by

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The following individuals read and discussed the thesis submitted by student Juliette Rubin, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

I would like to dedicate this thesis to my incredible team of bats, who unwillingly but devotedly gave their time. Also to the moths of the world, may you forever grow in beauty and educate our populace on the facts of evolution.

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ABSTRACT

Prey-generated illusions span sensory systems. Previous studies have mainly focused on visual illusions presented by prey coloring or morphology, but few have explored illusions produced via sound. We investigate an acoustic sensory illusion in moths, created by complex hindwing structures that divert echolocating bat predators. A phylogeny of the moth family, Saturniidae, in combination with data from geometric morphometrics, reveals that hindwings have repeatedly elongated to form tails across evolutionary time. Using high-speed, multi-camera, synchronized videos of bat-moth battles, we quantified the selective pressure of predation on extant and experimentally-modified moths, defined by moth escape success from bat attack. We approximated a gradient of less derived to more derived non-tailed Saturniidae morphs using *Antheraea polyphemus,* by reducing hindwing area (reduced), maintaining hindwing area (intact, sham) and adding hindwing area (elongated). We performed similar alterations along a potential evolutionary gradient with two tailed species, *Actias luna* and *Argema mimosae*, by removing the tails (ablated), shortening the tails (shortened, blunt), maintaining the tails (intact, sham) or elongating the tails (elongated, *A. luna* only). With increasing tail length, moths had a greater chance of surviving bat attack (model slope = 0.18±0.05) and the longest-tailed moths (tails > 7cm) survived bat attack in more than 56% of battles. Bat attack was also diverted from a moth's body to its hindwing region at increasing rates with increasing hindwing length (model slope = 0.31±0.05). Tailed moths drew bat attack either towards the body or tail ends in 75% of interactions and towards the hindwing in only 25% of interactions, thus providing support for an attack on multiple targets, rather than the center of a single enlarged echo. We also extracted the 3D flight paths of moths from these encounters and found that flight kinematics do not change across genera or treatments, nor are they associated with escape success. These data provide evidence supporting a sonar-specific sensory illusion of multiple targets, and a challenge to the physiological limits of bat echolocation.

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IPI	Interpulse interval

STUDY PREFACE

Predation is a potent selective pressure. Dawkins and Krebs hypothesize in their "life-dinner principle" (Dawkins and Krebs 1979), that the stakes in a predator-prey interaction are much higher for the prey than the predator. Predation is likely to have a strong role in shaping trait characteristics and behavior of prey animals. From under this selective pressure, diverse anti-predator adaptations can emerge (Vamosi 2005). My study focused on a potential evolutionary pathway that Lepidopteran (Order: moths and butterflies) lineages follow under natural selection from bat predation. Unsuccessful predation attempts are common among predatory mammals, around 50% post-detection (Vermeij 1982), and any trait that increases escape success for individual prey can be crucial. Research into the evolutionary pathways of both anti-predator and sexual traits indicate that intermediate trait values are often less advantageous than a complete absence or exaggeration of the trait. Thus, evolutionary stabilization might drive divergence (Emlen and Nijhout 2000; Buskirk et al. 2003; Langerhans 2007).

From a foundational study carried out by the Barber and Kawahara teams (Barber et al. 2015), we know that the hindwing tails of moths within Saturniidae provide a survival advantage against echolocating bats over non-tailed hindwings. Phylogenetic and geometric morphometric data indicates an apparent evolutionary progression of hindwing length within several clades, possibly from simple hindwings, to hindwing lobing, then from shorter to longer tails (Barber et al. 2015; Zhong et al. 2016). We therefore predicted that predation success would decline along this morphological continuum, and would drive the elongation of the hindwing tail trait, rather than stabilize the tailed and non-tailed forms. Because of their less vital role in flight (Jantzen and Eisner 2008), hindwings are likely more responsive to natural selection pressures than forewings (Outomuro et al. 2012). We experimentally tested the strength of predatory force imposed by bats against saturniids of varying hindwing lengths and structures, and paired these data with a phylogenetic view of hindwing evolution.

Bats and moths have been coevolving for the past 65 million years (Conner and Corcoran 2012). Since bats evolved laryngeal echolocation and powered flight (Gunnell and Simmons 2005), night-flying insects have been under attack. Long-lived moths must evade predation for weeks or months. Some moths in the family Sphingidae, for instance, must survive this nightly threat repeatedly as they complete their adult life cycle – nectaring and finding mates (Haber and Frankie 1989). These animals often have complex anti-bat behavior, driven by sonar detecting ears and sound producing structures (Miller and Surlykke 2001; Barber and Kawahara 2013). Sound production is a post-detection defense, which either startles the attacking bat (Bates and Fenton 1990), warns of moth toxicity (Dowdy and Conner 2016), mimics toxic moth sounds (Barber and Conner 2007), or jams bat sonar (Corcoran et al. 2009).

Saturniids have an entirely different strategy. This family comprises earless moths that lack sound producing structures and live only one week without feeding (Tuskes et al. 1996). Male saturniid moths need only run the nocturnal gauntlet for a few nights, weaving through the air to follow the pheromone trails of awaiting females (Cardé 2016). During these amorous flights, saturniid moths can dodge bat predation either by flying close to vegetation in the “clutter overlap zone” (Rydell 1998; Denzinger and Schnitzler

2013), or by flying at different times than bats (Yack 1988; Soutar and Fullard 2004). These conditions are spatially and temporally constraining, and rely on bats' failure to detect moths due to partitioning in time and space. Post-detection defenses, however, permit freedom of movement and allow for more direct, efficient flight between locations (Ratcliffe et al. 2008). Barber et al. (2015) describe a post-detection anti-bat trait in Saturniidae that has evolved repeatedly across clades. Hindwing tails with twisted and cupped ends that rotate in flight divert bat attack in 55.2% of interactions. In the current study, we investigate the proximate causes (Tinbergen 1963) for this deflective defense, and explore its role as a sensory illusion.

Sensory illusions "act to distort the perception of the viewer" (Kelley and Kelley 2014). This line of research therefore lends itself to understanding not just the evolutionary history of an illusory trait in the sender, but also the cognitive processing and constraints of the receiver (Théry 2014). Illusions have primarily been studied in human systems (Kelley and Kelley 2014), likely due to our own sensory constraints, which limit the type of sensory information and illusions that we can perceive. To document a sensory illusion, we must know enough about the receiver's sensory experience that we can predict how a sender might render information along a specific channel such that the receiver perceives something that does not exist (Merilaita 2014). Only with the advent of specialized equipment were scientists able to discern UV color patterns that flowers used to communicate with bees (Chittka et al. 1994). One might imagine, then, that documenting a misleading illusion in a foreign sensory system could be a difficult task. Humans primarily receive information through the visual system, and therefore most studies on sensory illusions focus on visual illusion (Kelley and Kelley

2014). There is overlap in visual illusions across human and non-human animals. Bowerbirds and humans share a susceptibility to the Müller-Lyer illusion; an illusion of forced perspective. Male bowerbirds organize objects along a positive size-distance gradient. That is, the court's components increase in size as distance from the bower increases, making the objects that the male displays on the court more salient to the female observer (Endler et al. 2010; Kelley and Endler 2012).

Acoustic illusions, such as "auditory induction," where the listener can restore components of an auditory segment that was erased by noise (Bashford and Warren 1987), are also present in the human sensory system and might be even more critical in acoustically oriented animals. Bat echolocation, although well studied, remains mysterious in some of its processing details and constraints (Griffon 1995; Yovel et al. 2011). This study seeks to probe the limits of echolocation through its investigation of an anti-bat sensory illusion in moths. I use a behavioral assay and phylogenetic evidence to track the evolution of elongated and structured hindwings, and their effect on bats. My data are just the beginning of a deeper understanding of a complex, ever-unfolding evolutionary story as bats and moths continue to clash fates across the night skies of almost every continent in the world.

THE EVOLUTION OF ANTI-BAT SENSORY ILLUSIONS IN MOTHS

Once detected by predators, prey must overpower, outrun, or redirect their attackers (Edmunds 1974; Cooper, Jr. 1998). To divert predatory strikes, prey manipulate predator perception (Kelley and Kelley 2014). Sensory illusions selected to misdirect predation attempts often target the primary sensory system of the predator (Stevens 2013; White and Kemp 2015). Conspicuous eyespots along butterfly wing margins (Lyytinen et al. 2003; Olofsson et al. 2010; Prudic et al. 2015) and brightly colored, waving lizard tails (Telemeco et al. 2011; Fresnillo et al. 2015) deflect strikes by visual predators away from the body. Sea hares eject ink that their chemosensory-oriented crustacean predators pursue as alternative prey (Kicklighter et al. 2005).

Moths navigate the nightly dangers of an auditory world, imposed by their echolocating bat predators. Recent work with moths in the family Saturniidae indicates that spinning hindwing tails divert bat attack away from the vital body core (Barber et al. 2015). These trailing structures seem to create an acoustic sensory illusion, distracting bats from their primary target, or displacing the echoic target center (Janzen 1984; Lee and Moss 2016). Tails have evolved in Saturniidae at least four different times, on three unique continent systems (*Actias* group [Saturniinae], Asia; *Eudaemonia* group [Saturniinae], Africa; *Copiopteryx* group [Arsenurinae], South America; *Coscinocera* group [Saturniinae], Australia). Each evolution contains a history of increasing hindwing length and complexity (Figure 1) (Barber et al. 2015). Geometric morphometrics on extant saturniids reveals a clustering into repeated morphological groups, with increasingly derived species moving from reduced hindwing area through enlarged hindwing lobes, to short projections, and eventually to elongated tails (Barber et al. 2015; Zhong et al. 2016). Hindwings might be more susceptible to evolutionary modification than forewings (Outomuro et al. 2012) because they are less constrained by flight requirements. A study testing the relative roles of insect wings found that complete removal of the hindwings mainly limits maneuverability, while forewing removal renders the animal flightless (Jantzen and Eisner 2008). Thus, although strikes to the moth's hindwing might be costly, structural damage to the forewing or body could be deadly. Hindwing morphology might therefore be released to expand into a more diverse morphometric space, driven by sonar sensing in attacking bats.

We address the proximate causes (Tinbergen 1963) of hindwing tails by measuring flight kinematics and natural selection of several hindwing shapes in an experimental paradigm. We pit 16 big brown bats (*Eptesicus fuscus*) against saturniid moths, both extant tailed and tailless species, and moths with experimentally-altered hindwing lengths (Picture 2). To measure the efficacy of moth tails as an anti-bat sensory illusion, we filmed bat-moth battles in a completely dark $10m^3$ sound-attenuating flight room. We used three synchronized high-speed cameras and four ultrasonic microphones trained on an interaction area defined by the flight range of a moth constrained by a 1m fishing line tether.

To track the potential non-tailed precursory stages of this sensory illusion, we simulated reduced-hindwing and derived elongated-hindwing conditions in the polyphemus moth (*Antheraea polyphemus*) by cutting and gluing the hindwing material. We built Bayesian models, including moth size as a covariate, individual bat identity as random slopes and bat hunting night as random intercepts to focus our analysis on the outcome of bat-moth battles. Polyphemus with experimentally elongated hindwing lobes escape bat attack more often than intact polyphemus (hindwing length elongated = 5.8±0.40cm [mean±SD], escape success=56%±0.11; hindwing length intact = 5.4±0.29cm, escape success = 27%±0.09) (Figure 2). While we found no difference in escape success between polyphemus with experimentally reduced hindwing area (hindwing length reduced = 3.34±0.32, escape success = 45%±0.10) and intact polyphemus moths (27%±0.09), bats directed more of their strikes toward the hindwings of elongated polyphemus moths (proportion of strikes towards posterior region of elongated = 50%±0.11) than any of the other treatments' (intact = 17%±0.08, reduced = 12±0.05) (Figure 3A). Our behavioral paradigm provides evidence that elongated hindwing lobing deflects bat attack.

To understand the anti-bat advantage that twisted and cupped tails offer in addition to hindwing lobing, we experimentally varied tail length in naturally tailed luna (*Actias luna*, tail length = 7.26±0.59cm) and African moon moths (*Argema mimosae*, tail length = 12.32±0.77cm), and pit these treatments against the same bats. With complete removal of a tail, escape success was low (ablated luna hindwing length = 4.0±0.32cm, escape success = 26%±0.09; ablated moon moth hindwing length = 5.04±0.23cm, escape success = 34%±0.13) (Figure 2), and bats infrequently aimed their attacks at moth hindwings (proportion of posterior attacks on ablated luna = 17%±0.07, ablated moon moth = 18%±0.10) (Figure 3A). We created short-tailed luna (tail length = 5.09±0.47cm) and moon moths (tail length = 8.55±0.34cm) by removing the tail shafts and regluing the twisted and cupped ends to the hindwing. Short-tailed luna escape more than ablated luna (short-tailed = 60%±0.09, ablated = 26%±0.09). We did not find the same result in moon moths (short-tailed = 45%±0.13, ablated = 34%±0.13), although this could be attributed to low sample size (*n* short-tailed = 22, *n* ablated = 17, Figure 2), particularly given that moon moths follow the same positive trend of the complete escape model (total escape model slope = 0.18 ±0.05) (Figure 2).

The process of cutting and gluing tail material did not in itself change flight ability, or proficiency at evading attacking bats. Control sham treatments, with hindwing area or tails cut and re-glued (Picture 2), yielded the same escape success (sham polyphemus = 43%±0.11, sham luna = 57%±0.11, sham moon moth = 78%±0.12) and drew the same proportion of bat attacks to the hindwing region (sham polyphemus = 18%±0.08, sham luna = 41%±0.11, sham moon moth = 61%±0.14) as intact animals of each genus. Three-dimensional kinematic analyses derived from synchronized high-speed footage of intact and sham moths in flight revealed no difference in mean speed, tangential acceleration, angular velocity, or their correlated counterparts (mean curvature, radial acceleration and tortuosity; *n* = 8-12 per treatment). Reducing and elongating the hindwing material of moths also did not affect flight kinematics (*n* = 10-13), except in short-tail moon moths, which had a larger mean angular velocity (turning rate *sensu* (Combes et al. 2012)) than intact moon moths (Table 1.1). Previous studies report that angular velocity is an important variable for prey escape (Combes et al. 2012; Corcoran and Conner 2016). Short-tailed moon moths were not different from intact moon moths in evading bat attack, however (Figure 2). Our Bayesian model revealed no correlation between mean angular velocity and escape success, and no change in the direction of the model slope (Table A1). We therefore excluded angular velocity from our models and do not attribute evasion differences between treatments to the hindwing modification methodology, or to flight parameters in the resulting morphs.

In aggregate, escape success increases markedly with increasing hindwing length (escape model slope = 0.18±0.05). We find the same result when we remove moon moths, whose long tails provide an impressive effect, from the model (escape model slope with moon moths removed = 0.17±0.06, Table A2). Intact moon moths escape bat attack markedly more than short-tailed or ablated morphs (intact escape success = 73%±0.09, short-tailed = 45%±0.13, ablated = 34%±0.13) (Figure 2). Luna moths have more incremental variations in escape success between treatments, yet track the same positive trend as the overall models, where escape success (total escape model slope = 0.18±0.05) (Figure 2), and diversion of bat attack (total posterior aim model slope = 0.31±0.05) (Figure 3A) increases with hindwing length. The moon moth is a larger animal than the luna moth, with tails 1.5 times longer. Although our models control for moth size, moon moth's twisted and cupped ends take up one third of the total tail length, while lunas' make up one half. Thus, although changes to tail length were proportionally the same, (moon moth short tail 69% of intact tail, luna moth short tail 70% of intact tail), alterations to moon moth tails maintain a greater positional distance from the body center, and might therefore have produced greater effect. Clearly, longer hindwing tails provide a powerful anti-bat advantage.

Tails could alter a bat's perception of the echoic target of a moth (Barber et al. 2015), either via an illusion of larger size (Janzen 1984), due to an integration of echo highlights reflected across the moth's entire length to create an enlarged echo with a target center shifted from the true moth center (Lee and Moss 2016), or due to the creation of two or more alternative targets created by primary reflections from the forewings and cupped ends of the tails (Fig. 3B inset). Our behavioral results indicate that bats hunting tailed moths targeted either the body or the ends of tails 75% of the time, providing support for a multiple targets illusion (Fig. 3B). A similar illusion is generated in the visual system, when bird attacks are drawn from the head and anterior wing margins (Wourms and Wasserman 1985) to deceptive “false heads” twitching at the tips of butterflies’ hindwings (Robbins 1981; Stevens 2005; Sourakov 2013).

To begin to understand the morphology underlying tails’ diversionary effect, we removed the twisted and cupped ends of luna tails, creating a blunt-tailed morph. These blunt ends exist naturally in butterflies and day-flying moths with short, unstructured tails (Scoble 1992). Blunt luna and shortened luna provide a good comparison because the length of extra hindwing material is roughly the same, but shortened luna maintain the end structure (Blunt length = 5.67±0.42cm, short-tail length = 5.09±0.47cm). We found that both these morphs escaped bat attack (blunt-tailed = 50%±0.10, short-tailed = 60%±0.09) (Fig. 2), and diverted bat aim to the posterior region with roughly the same rate (blunt-tailed = 23%±0.08, short-tailed = 37%±0.09) (Figure 3A). With longer tails possessing twisted and cupped ends, intact luna moths are more successful at diverting bat attack to the hindwing region than blunt luna moths (intact = 45%±0.08, blunt-tailed = 23%±0.08). This difference is not solely reliant on tail length, however, since there is no measurable difference in the proportion of posterior attacks between intact luna and shortened luna (intact = 45%±0.08, shortened = 37%±0.09), despite intact luna having longer tails. Thus, the efficacy of the illusion relies to a certain degree on the twisted end of the tail.

How elongated hindwings create an acoustic illusion likely depends on the sonar strategy and processing limitations of the attacking bat. Moths face a diversity of bat species and echolocation types on a given night (Denzinger and Schnitzler 2013). Bats with frequency modulated sonar cries, such as *E. fuscus*, might extract object characteristics from a single echo (Grossetête and Moss 1998; Yovel et al. 2011), or across an echo stream (Kober and Schnitzler 1990a; Moss and Zagaeski 1994; Fontaine and Peremans 2011). Constant frequency bats are known to use Doppler shifts imposed on the returning echo stream to discriminate targets (Von Der Emde and Schnitzler 1990; Kober and Schnitzler 1990b). It is possible that spinning hindwing tails create a flutter signature in constant frequency echoes distinct from the fluttering moth forewings, but it is unclear whether tails would have the same effect for frequency modulated bats. Definitively determining the illusion created by rotating hindwing tails awaits phylogenetically widespread, multi-angle ensonification experiments, using both constant frequency and frequency modulated sonar regimes, to generate a three-dimensional reconstruction of the perceived moth shape from all possible attack angles.

Regardless of the mechanism, elongated tails clearly tested the physiological limits of our frequency modulated bats' processing ability. Over months of hunting nights and interactions with tailed animals, bats' strike accuracy and capture success did not improve (Table 1.2). Additionally, we did not find any differences in the sonar behavior of bats across moth treatment (Figure A1, A2). FM bats elongate the duration of their terminal sonar phases (buzz I and buzz II) when confronted with a more difficult predatory task (Hulgard and Ratcliffe 2016). We did not observe any changes in buzz duration, indicating that the bats in our study did not perceive a task difficulty gradient among the moth morphs we presented.

Bats experienced the same difficulty capturing moths with experimentally elongated lobing as moths with tails (Fig. 2). Our study did not address post-capture handling, and therefore survival, which could vary between a large hindwing and structured tail morphology (Wourms and Wasserman 1985; Eschke and Opp 2002). Tails might provide a similar deflective effect to elongated lobing, but offer less material for an attacking bat to grab during aerobatic capture maneuvers. In contrast to lobing, the smaller surface area of tails might also reduce energetic requirements for the moth pupa during development (Miner et al. 2000), or might provide a flight benefit, shedding air vortices during flight to improve maneuverability (Evans and Thomas 1992; Norberg 1994). Their aerodynamic structure might additionally enhance maximum vertical aerodynamic force production and maximum power output, although the added weight and possible drag could also have energetic costs (Marden 1994; Chai et al. 1997; Dillon and Dudley 2004). Our kinematic assessments did not reveal differences in flight ability between tailed (luna, moon moth) and non-tailed (polyphemus moth) genera (Table 1.1), and therefore did not support a flight benefit to tails, but this question deserves more study. In lineages that have evolved tails, their length and structure might play a role in sexual selection, although saturniids are short-lived and females tend to mate with the first male that approaches (Morton 2009). Perhaps simply surviving the predatory hazards of night flight is evidence enough for a male’s superior genetics and efficacy at generating an anti-bat illusion.

Bats could evolve a counter-measure to shatter moths' acoustic illusions. Perhaps this already occurs in the night sky, where bats have access to visual cues provided by moonlight (Boonman et al. 2013). Interestingly, moon moth tail shafts are dark in color, with only the twist and cupped tail ends sharing the same bright green as the moth's fore and hindwings. This dichromatic patterning could visually augment the acoustic illusion of moth tail ends as alternative targets to the moth body. Acoustic illusions could also exist in other forms. Moth scales absorb ultrasound within the frequency range of their bat predators (Zeng et al. 2011), which might cause the bat to misjudge target distance (Ntelezos et al. 2016), or misconstrue the true shape of the moth. We predict that sensory illusions are widespread defenses throughout predator-prey systems, and provide a novel means of probing the evolutionary edge of predator processing.

Materials and Methods

Behavioral Methods:

We conducted all studies in a dark 10m^3, sound-attenuating flight room at Boise State University. Illumination was provided to researchers and cameras by two red ceiling lights and eight infrared Wildlife Engineering arrays. We filmed all interactions with three synchronized, high-speed, infrared-sensitive cameras (Basler Scout, 120fps, 3.5mm lens) and an additional Basler Scout camera was fitted with a 6mm lens for a narrower focus to aid in behavioral identification. Before beginning their experimental trials, we allowed bats two weeks post-capture to acclimate to the novel lab setting. We trained bats to approach a 1m monofilament line secured to the ceiling by stringing wax moths (*Grisella mellonella*) during each flight session. Vitamin-coated meal worms and water *ad libidum* supplemented bats' diets. Once a bat could catch wax moths off the line with 90-100% success, we introduced 1-2 saturniids a day. We did not consider bats ready to begin the experimentation process until they seemed motivated to repeatedly attack saturniids.

Once a bat was ready for trials, we introduced experimental moths in randomized order, commonly resulting in each bat hunting different moth species of varying treatments each night. We presented two small pyralids (*Grisella mellonella*) in pseudo-randomized order, one at the beginning of the experimental day and one partway through the trial, to ensure bat motivation levels were high. Before allowing the bat to attack, we verified that moths were adequately flying. We suspended the trial if a moth ceased flying, or if damage occurred. Upon review of the triple video recordings, we eliminated all moths exhibiting unnatural flight from the dataset. Each day we inspected newly eclosed moths for eclosion defects or damage before pitting them against bats. We assigned each approved moth one of several possible hindwing alteration treatments and photographed it against graph paper for size analysis before the trial began. We created the various treatments by cutting and gluing hindwing material to shorten or lengthen posterior structures (Picture 2). Vertebrate work was done following Boise State University's Animal Care and Use Committee protocol (number: 006-AC14-018).

We completed behavioral analysis using a custom built LabView program and Maxtraq. J.J.R. surveyed all footage and noted the behavior type (capture, aim, miss, and location of damage on the moth's wings, if applicable) and time stamp within the video for each interaction so that audio and video data could be analyzed together. We defined *Capture* behaviors as the bat being able to grab and carry the moth out of the interaction space. *Aim* behaviors was the directional heading of the bat at either the forewing and body (anterior) or hindwing (posterior) of the moth three frames before the interaction. We included tail end aim as an additional category for moths with long tails (*A. luna* intact, sham, elongated; *A. mimosae* short, intact, sham). *Miss* we defined as a bat making no contact with the moth, despite exhibiting complete capture behaviors, including full attack echolocation call and enclosure of the wing membrane. We determined the location of bat-related damage by visually inspecting the video, as well as post-encounter photos that we took after a damaging attack.

Statistical Analysis

We used generalized linear mixed models fit under a Bayesian framework to examine differences between treatment groups and relationships between dependent variables and tail length. To determine differences between treatments, we used models including treatment as a fixed factor. To determine relationships with tail length, we used models that included tail length as a covariate. We implemented the model in JAGS version 4.2.0 (Plummer 2003) using the jagsUI package version 1.4.4 (Kellner 2016) and R version 3.2.3 (R Core Team 2016). We ran 3 chains for 50,000 iterations after 10,000 burnins. We used standard weakly informative priors (Kéry and Schaub 2012) and visually assessed traceplots and used the Gelman-Rubin statistic (Gelman and Rubin 1992) to check for convergence. We built escape and aim models with binomial distributions and logit links. To focus our conclusions on natural selection forces, we included moth size as a covariate and individual bat identity and hunting night as random intercepts and slopes, respectively.

Kinematic Analysis

We randomly selected ten videos from each treatment for digitization, beginning 100 frames (1 second) out from the moment of bat-moth interaction. When possible, we did not digitize an individual moth’s flight path more than once, even if it contributed multiple trials to our dataset. We were only able to digitize eight sham *A. mimosae* flights, due to camera view obstruction (i.e., moth flew behind one of the mounted microphones, or researcher’s hand obscured the flight path). We recorded trial number for each moth and determined that it was statistically inconsequential to flight kinematics. Using DLTdv5 and easyWand5 packages in MATLAB (Hedrick 2008; Theriault et al. 2014) we digitized moth flight from our recorded bat-moth interactions on the tether, with center of moth body as our focal point. We ran our outputs through a custom-built MATLAB package, Moth Drop (written by B.A.C), and extracted flight parameters of interest for evading predatory capture, as defined per Combes et al. (2012). After running a correlation matrix (R package Hmisc), we found that mean speed, mean tangential acceleration and mean angular velocity were uncorrelated with each other, but highly correlated (>0.7) with one or more of the other variables. We therefore limited our comparisons to include only these three parameters. Angular velocity (correlated with tortuosity and mean curvature) was different between the intact *Argema* and shortened *Argema* treatments. We ran models of moth escape success against bats including and excluding the mean angular velocity parameter to determine whether this flight difference affected interaction outcome. We built models with normal distributions and identity links and included moth size as a covariate and random slopes and intercepts for hunting night and individual bat identity to control for different hunting and learning abilities.

Including kinematic parameters does not provide a different explanation of the data, or a better inference capability for the model.

Audio analysis

We acoustically recorded all attack sequences using four ultrasonic Avisoft microphones (CM 16, ±3dB(Z), 20-140 kHz) surrounding the interaction space in the four cardinal directions. We analyzed the resulting files using Avisoft SASLab Pro software (Hann Window, 1024 FFT). For each moth treatment, we analyzed between 10-15 call sequences, using 1-2 sound files from at least three different bat individuals. When possible, we selected one file from an initial hunting trial and one file from a later hunting trial for each bat to account for diversity of experience. We inspected all audio channels, beginning 900ms back from the selected interaction, and chose the channel with the highest signal to noise ratio to analyze (as in Barber et al. 2015). This selection always included pulses from the approach (IPI >15ms), Buzz I (IPI ≤15ms) and Buzz II (IPI ≤6.5ms) phases (Griffin et al. 1960; Geberl et al. 2015). Buzz I and II are together considered the terminal phase of an echolocation attack sequence and provide the bat the final details of a prey animal’s flight path through an increase in pulse emission rate, a decrease of interpulse interval (IPI) and a broadening of the frequency bandwidth, and therefore beam, of the call (Jakobsen and Surlykke 2010; Ratcliffe et al. 2013; Geberl et al. 2015). We included random slopes and intercepts for individual bats to control for different hunting and learning abilities. All acoustic models included the size of individual moths as covariates. We found no difference in buzz duration lengths while hunting tailed versus non-tailed moths. Using the power spectra function in SASLab Pro, we extracted the frequencies at 15dB below and above the frequency at peak amplitude in

Buzz II (Surlykke and Moss 2000) and using the frequency cursor tool, we extracted the absolute minimum frequency of Buzz II. We found no differences in these frequency measurements.

Moth size analysis

We photographed each moth in the dataset after completing its treatment and before flying it against a bat. Later, we measured the surface area and hindwing length of each moth from these photos using the freehand and straight line drawing tools, respectively, in the freely downloadable program ImageJ (https://imagej.nih.gov/ij/). We included individual moth surface area as a covariate in the model and maintained hindwing lengths as a primary predictor.

CONCLUSION

My experimental behavioral data, together with phylogenetic evidence, provide a path and a mechanism by which a sensory illusion has likely evolved. Given our behavioral data and the multiple independent origins of this trait, elongated hindwing tails seem to be an effective post-detection anti-bat strategy in moths. I found that a tail of any length brought predator success to 50% or less. This is a standard rate for predator attack (Vermeij 1982), and in the context of the life-dinner principle (Dawkins and Krebs 1979), still makes any night flight a risky business for a saturniid moth. As tails get longer, the slope of the escape success curve moves in a positive direction. Even while accounting for body size, *A. mimosae* moths with some of the longest tails in Saturniidae evade capture by bats at a rate that rivals sonar-jamming Sphingidae moths (~50-90% in *Xylophanes falco*, *Xylophanes tersa*) (Kawahara and Barber 2015).

Considerations for future study

Our data indicate that saturniid moths produce a distractive sensory illusion, where the bat misconstrues spinning hindwing tails to be an alternative target to the body center. More research is needed at this point to determine exactly how this illusion is generated. Sensory illusions can provide a rich line of study because of their implications for understanding anti-predator defenses in prey, as well as the cognitive limits of predators. Studying these anti-predator defenses gets at the core of the sensory ecology field, which aims to understand the umwelt of an organism (Uexküll 1910), that is, how an animal receives and responds to information about the world, due to its unique assemblage of senses (Dangles et al. 2009).

One novel method for understanding a bat's umwelt is ensonification. Ensonification experiments involve projecting ultrasonic frequencies at an object and recording the returning echoes to get a glimpse of a bat's perception. This has been done with moth tails (Lee and Moss 2016), however, to get a full understanding of an attacking bat's perspective we would need to use multi-microphone arrays and ensonify live moths from all incident angles. During wild, aerobatic chase sequences bats might perceive tails differently, as they ensonify the moth from various directions (Simmons and Chen 1989). Although ensonification can offer an approximation of first-hand echolocation experience, a full understanding of bat perception awaits more fine-scaled research into how bats process sonar images (Fenton 2013).

It will also be crucial to conduct more bat-moth studies *in situ*, capturing natural encounters between predator and prey across the Old and New World tropics. Filming must be done with high resolution cameras so that we can visually track, and reliably digitize, the complex flight maneuvers executed by bats and moths. Wild filming could additionally provide insight into important natural history questions surrounding these interactions, including the maximum speed and curvature the animals can reach when there are no space constraints (Betts and Wootton 1988; Ellington 1991), and the level in the canopy that interactions occur (Schulze et al. 2001). These factors are important for understanding ultimate flight capability and the specific species pairings that interlock in predator-prey battles. Acoustic recordings of free-flight battles could also shed light onto the strategies that bats use while hunting saturniid moths. It is already known that bats modify their echolocation calls slightly in a controlled flight room (Surlykke and Moss 2000). It will therefore be important to record echolocation calls during wild attacks, when the bat is forced to hunt while simultaneously navigating the complexities of a natural forest environment. With this knowledge, we could more easily contextualize our laboratory findings within an ecological and evolutionary framework.

To obtain a more holistic view of anti-bat hindwing morphology, it will also be important to determine whether complex hindwings have any role in mating success. Saturniids are often monandrous (mating with the first male that approaches) (Tuskes et al. 1996; Morton 2009), however some species might select mates based trait assessment (Torres-Vila and Jennions 2005). Preliminary results from a collaborative study in the Barber and Kawahara labs indicate that female luna moths do not prefer to mate with tailed males versus ablated males, but this system calls for more in-depth study. Although some tailed saturniid species exhibit sex-based morphology differences, where females don't possess tails at all, both *A. luna* and *A. mimosae* females have tails comparable to males'. This would be unexpected if tails were costly and only males completed nuptial flights during hours of bat activity (Acharya 1995; Allen et al. 2011). Female saturniids do, however, fly relatively shorter distances than males to find a suitable spot to lay their eggs (Tuskes et al. 1996). Tails must thus either be a neutral trait, or provide an adaptive benefit to females. This question requires further natural history study, to determine when and how often females fly, and phylogenetic comparison between lineages with sexually dimorphic and monomorphic species.

Reproduction studies combined with predatory battles in the laboratory could provide a broader view into the elongated hindwing illusion. During my study, moths that were structurally (non-fatally) damaged by bat attack were retrieved, photographed and re-flown, when possible. These data were identified as “post-interaction” trials and were recorded, but never analyzed due to time constraints. With the appropriate quantification of the extent of damage to each moth, moths could be categorized and assigned to further “post-interaction” or mating trials. That is, animals that survived a damaging bat attack could either be pit against a bat again to determine subsequent survival success, or be introduced to a reproduction chamber to determine whether they would still successfully find and complete mating. Given the heritability and flexibility of wing traits, this kind of longer-term investment in individual moths could reveal whether pressures from varying factors influence evolutionary changes in saturniids (Bolstad et al. 2015; Allen 2016).

Notes on bat and moth study subjects

I chose big brown bats (*Eptesicus fuscus*) for the predator in my laboratory system for several reasons. First, this species is native to Idaho, and thus is easily attainable and releasable. Second, through diet analysis *Eptesicus* bats are known predators of Saturniidae and are representative of the general size of other bat predators to this family (15-20g) (Aguiar and Antonini 2008; Balete 2010). Third, *E. fuscus* on the eastern side of North America overlap with tailed *A. luna* moths. *Eptesicus fuscus* from Idaho, however, are ubiquitously naïve to this anti-bat strategy, which would have been important had we found evidence of bats learning how to successfully circumvent hindwing illusions. Last, these bats have well documented frequency modulated (FM) calls, which is a known strategy in aerial insectivores that hunt in open spaces (Simmons et al. 1998; Surlykke and Moss 2000; Schnitzler et al. 2003). For these reasons our experimental set up created a tractable and easily generalizable study. Future studies should include laboratory research with constant frequency bat species, that is, bats who hunt using flutter detection (Bell and Fenton 1984). Constant frequency echolocation is the predominant sonar strategy in the Old World (Neuweiler 2003), where several clades of tailed saturniids have diversified (Michener 1949). Understanding how the hindwing sensory illusion operates under this alternative sonar strategy will therefore be necessary to tracking its evolutionary path.

I chose *A. luna, A. mimosae* and *A. polyphemus* as my three representative species due to their grouping within one subfamily of Saturniidae (saturniinae) and their varying hindwing morphologies. *A. luna* and *A. polyphemus* are easily attainable moths, as they are charismatic species, regularly used in Lepidoptera exhibits and educational events. *A. mimosae* are larger and considered more exotic and therefore are more costly and difficult to acquire. Future studies would ideally have access to even larger funds and more expansive timelines so that more *A. mimosae* could be purchased to increase the sample size for some treatments and multi-generational studies could be carried out across all treatments. More funding would also allow for a greater diversity of hindwing morphologies to be tested, including short-tailed Saturniinae and lateral-tailed (projecting off a lateral vein) Arsenuriinae moths.

Final remarks

My data point to natural selection by bats as an evolutionary driver of hindwing elongation in nocturnal Saturniidae through phylogenetic time. There are similar evolutions of complex hindwing shapes in other moth families, including Sematuriidae and Uraniidae (Picture 3). In both of these independent origins, the tails are also twisted and cupped in a similar manner to saturniid morphology. Hindwings might be prone to structural modifications in response to bat predation pressure (Outomuro and Johansson 2015), due to their independent development from forewings during the pupal stage (Nijhout and Emlen 1998) and their less vital role in basic flight (Jantzen and Eisner 2008). Research describing beak damage and tear lines along conspicuous marginal markings on butterfly hindwings provides evidence that hindwings sometimes act in a role ancillary to flight (Hill and Vaca 2004). What's more, there is flexibility in resources distributed to wing building during development. When relieved of the energetic constraints of building four wings (by removing the two hindwing imaginal discs), the two remaining forewings wings will grow disproportionately large (Nijhout and Emlen 1998; Nijhout and Callier 2015). This sort of reallocation belies a plasticity of energy use and gene expression in Lepidoptera pupal stages. More work needs to be done with Saturniidae and other tailed moth families to determine the combination of factors that might lead to hindwing tails.

It is especially important to carefully construct studies in the future that will elucidate exactly how bats perceive the illusion created by hindwing tails (most likely via ensonification). Elongated *A. polyphemus* moths escaped bat attack with the same success as tailed animals, thus the question remains how elongated lobes function to deflect bat attack and whether it's by precisely the same means as spinning tails. Whether hindwing tails across genera function in the same manner is also an outstanding question. *A. mimosae*'s wing material has greater flexural stiffness than *A. luna*'s, which is common in larger insects (Combes and Daniel 2003). Its shafts are also thinner, longer and more brittle. These differences could potentially lead to differing illusory mechanisms, or could simply allow two differently shaped and sized animals to evoke the same sensory illusion. Research into the material properties of these wings, and how they function echoically, would reveal interesting results.

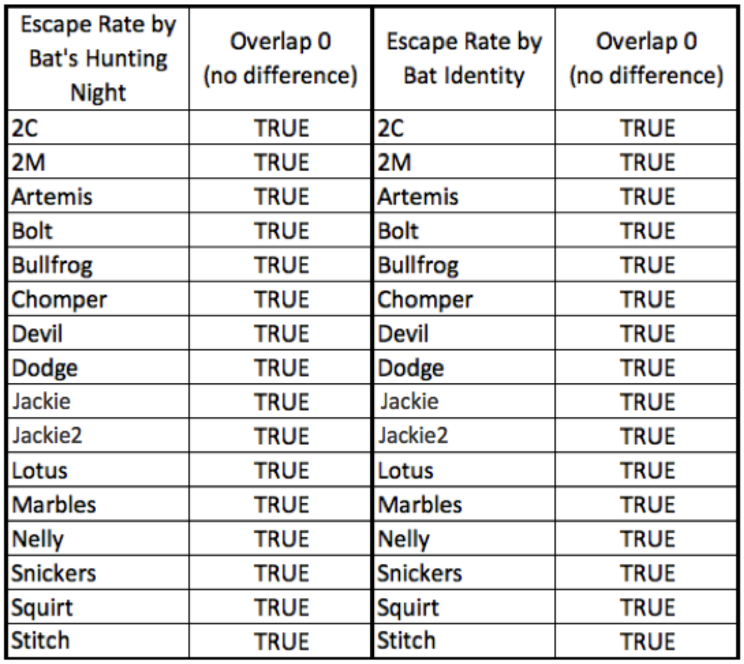
Sensory illusions provide a new conceptual framework to investigate the evolutionary drivers of trait characteristics. Organisms can only interact with each other and their external environment based on the constraints of their sensory profile (Stevens 2013). From this view, the researcher must probe the perceptual and reactionary palate of both predator and prey. There is still much more to know about bat and moth sensory processing. This system provides us with evidence for the limits of bat echolocation, and the exploitation of these constraints by moth prey across their evolutionary history.

Tables

Table 1.1 Kinematics. Kinematic output data from 100ms of tethered flight, using a custom-built Moth Drop program. All other parameters were correlated with mean speed, mean tangential acceleration and mean angular velocity (r_{ho}>0.7). Flight variables from each treatment compared with intact standards of the same species, outlined in black. Any differences between treatment moth values and intact moth values from the same species are highlighted in red.

	Mean Speed	Mean Tangential Acceleration	Mean Angular Velocity
Intact *A. mimosae*	mean=0.721 SD=(±0.096)	mean=0.029 SD=(±0.199)	mean=2.948 SD=(±0.61)
Sham *A. mimosae*	mean=0.845 SD=(±0.113)	mean=-0.141 SD=(±0.234)	mean=2.77 SD=(±0.713)
Shortened *A. mimosae*	mean=0.639 SD=(±0.097)	mean=-0.327 SD=(±0.198)	mean=4.72 SD=(±0.607)
Ablated *A. mimosae*	mean=0.475 SD=0.101	mean=-0.221 SD=(±0.208)	mean=3.119 SD=(±0.638)
Intact *A. luna*	mean=0.732 SD=(±0.101)	mean=-0.281 SD=(±0.209)	mean=4.066 SD=(±0.639)
Sham *A. luna*	mean=0.876 SD=(±0.093)	mean=-0.202 SD=(±0.191)	mean=3.631 SD=(±0.582)
Shortened *A. luna*	mean=0.902 SD=(±0.089)	mean=-0.165 SD=(±0.184)	mean=5.026 SD=(±0.56)
Blunt *A. luna*	mean=0.829 SD=0.101	mean=-0.721 SD=(±0.209)	mean=3.926 SD=(±0.637)
Ablated *A. luna*	mean=0.76 SD=0.101	mean=-0.121 SD=(±0.208)	mean=4.993 SD=(±0.637)
Elongated *A. luna*	mean=0.939 SD=0.101	mean=0.042 SD=(±0.208)	mean=4.608 SD=(±0.636)
Intact *A. polyphemus*	mean=0.671 SD=(±0.101)	mean=-0.122 SD=(±0.209)	mean=3.765 SD=(±0.638)
Sham *A. polyphemus*	mean=0.575 SD=(±0.101)	mean=-0.175 SD=0.208	mean=3.04 SD=(±0.637)
Ablated *A. polyphemus*	mean=0.661 SD=(±0.089)	mean=-0.024 SD=(±0.183)	mean=4.901 SD=(±0.558)
Elongated *A. polyphemus*	mean=0.686 SD=0.097	mean=0.089 SD=(±0.199)	mean=3.286 SD=(±0.607)

Table 1.2 Bat Identity and Experience with Saturniids Do Not Affect The Outcome of the Trial. Bats included as random intercepts and the number of nights bats spent hunting saturniids (bat experience) included as random slopes in a Bayesian model overlap 0, indicating that they do not have an effect on moth escape success.



Escape Rate by Bat's Hunting Night	Overlap 0 (no difference)	Escape Rate by Bat Identity	Overlap 0 (no difference)
2C	TRUE	2C	TRUE
2M	TRUE	2M	TRUE
Artemis	TRUE	Artemis	TRUE
Bolt	TRUE	Bolt	TRUE
Bullfrog	TRUE	Bullfrog	TRUE
Chomper	TRUE	Chomper	TRUE
Devil	TRUE	Devil	TRUE
Dodge	TRUE	Dodge	TRUE
Jackie	TRUE	Jackie	TRUE
Jackie2	TRUE	Jackie2	TRUE
Lotus	TRUE	Lotus	TRUE
Marbles	TRUE	Marbles	TRUE
Nelly	TRUE	Nelly	TRUE
Snickers	TRUE	Snickers	TRUE
Squirt	TRUE	Squirt	TRUE
Stitch	TRUE	Stitch	TRUE

Figures

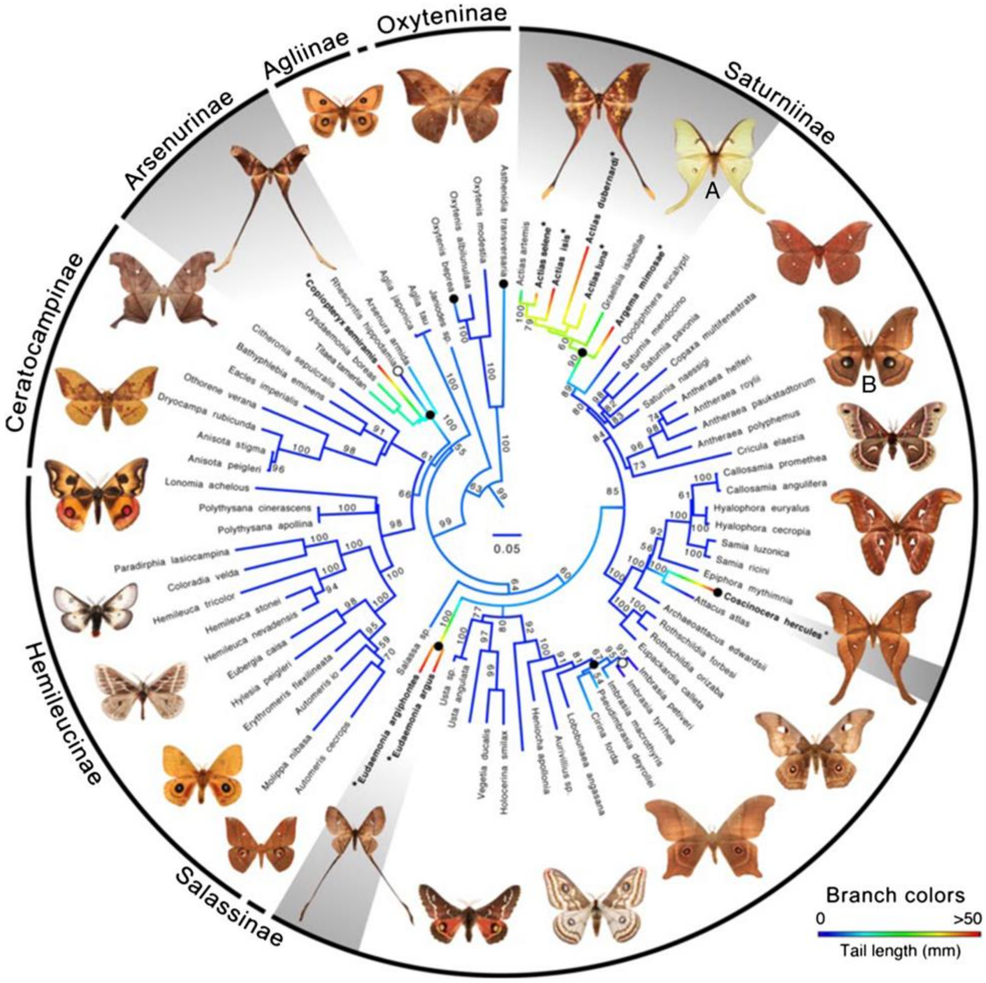


Figure 1. **Saturniidae Phylogeny. Molecular data from five nuclear loci and the COI mitochondrial gene for taxa from Saturniidae and related bombycoid families demonstrate four evolutions of hindwing tails with twisted and cupped ends (in gray highlights). Filled black circles are origination points for tails and open circles are tail losses. Warmer colors indicate longer tails, and asterisks indicate tails that are >3.75cm. Letters A and B in the figure represent moths that we used for the behavioral assay. Reprinted with permission from Barber et al. (2015).**

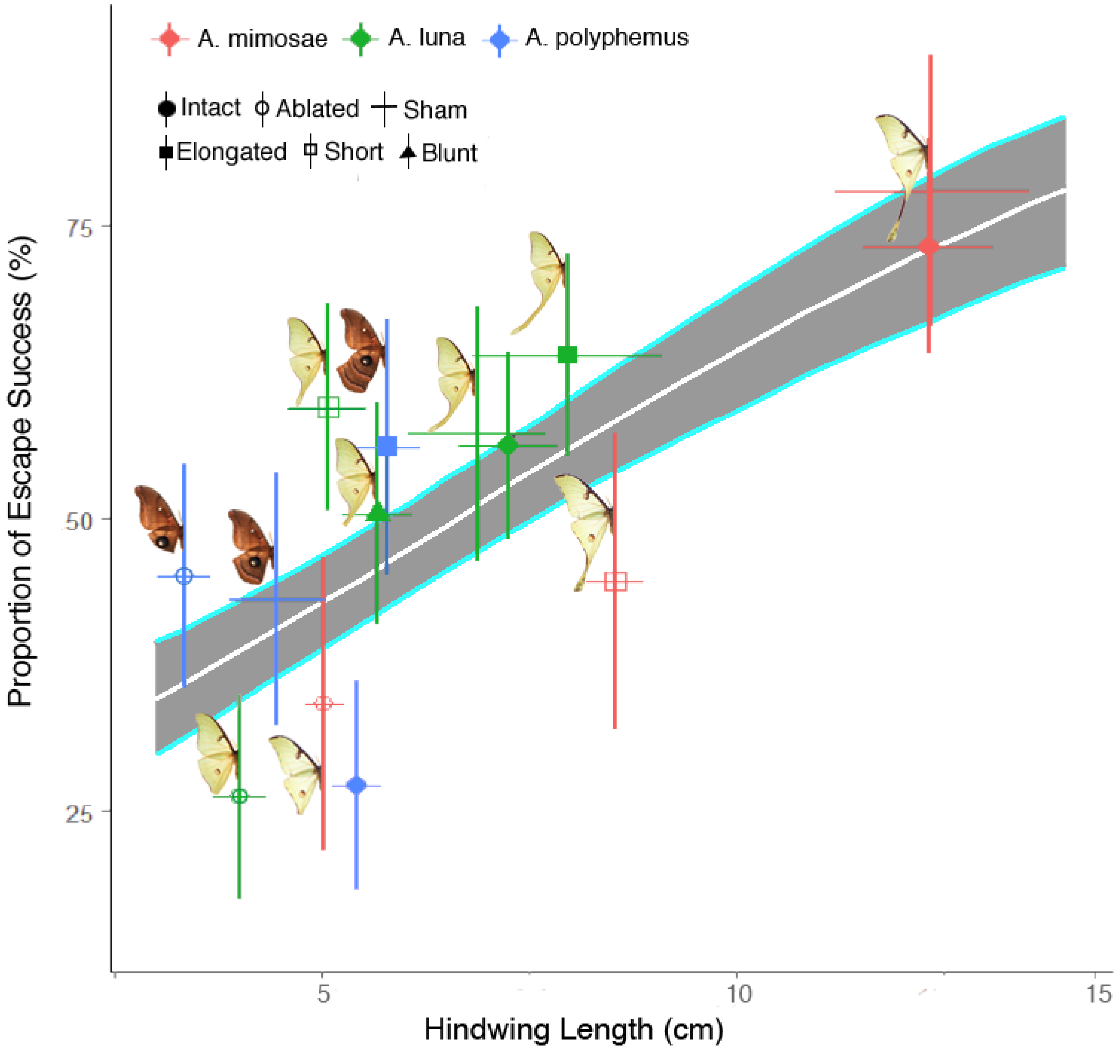


Figure 2. **Escape success. Bayesian model of the proportion of interactions where a moth escaped bat attack. Inner white line represents the model slope mean and the gray area is 95% credibility interval around the mean. Images of moth treatments are positioned on their respective data bracket. Only one picture is shown for an intact or sham, as they have the same morphology. Samples sizes are as follows: *A. mimosae* (ablated = 17, intact = 30, sham = 13, short = 22,); *A. luna* (ablated = 38, blunt = 48, elongated = 82, intact = 64, sham = 37, short = 93), *A. polyphemus* (ablated = 44, elongated = 29, intact = 40, sham = 35).**

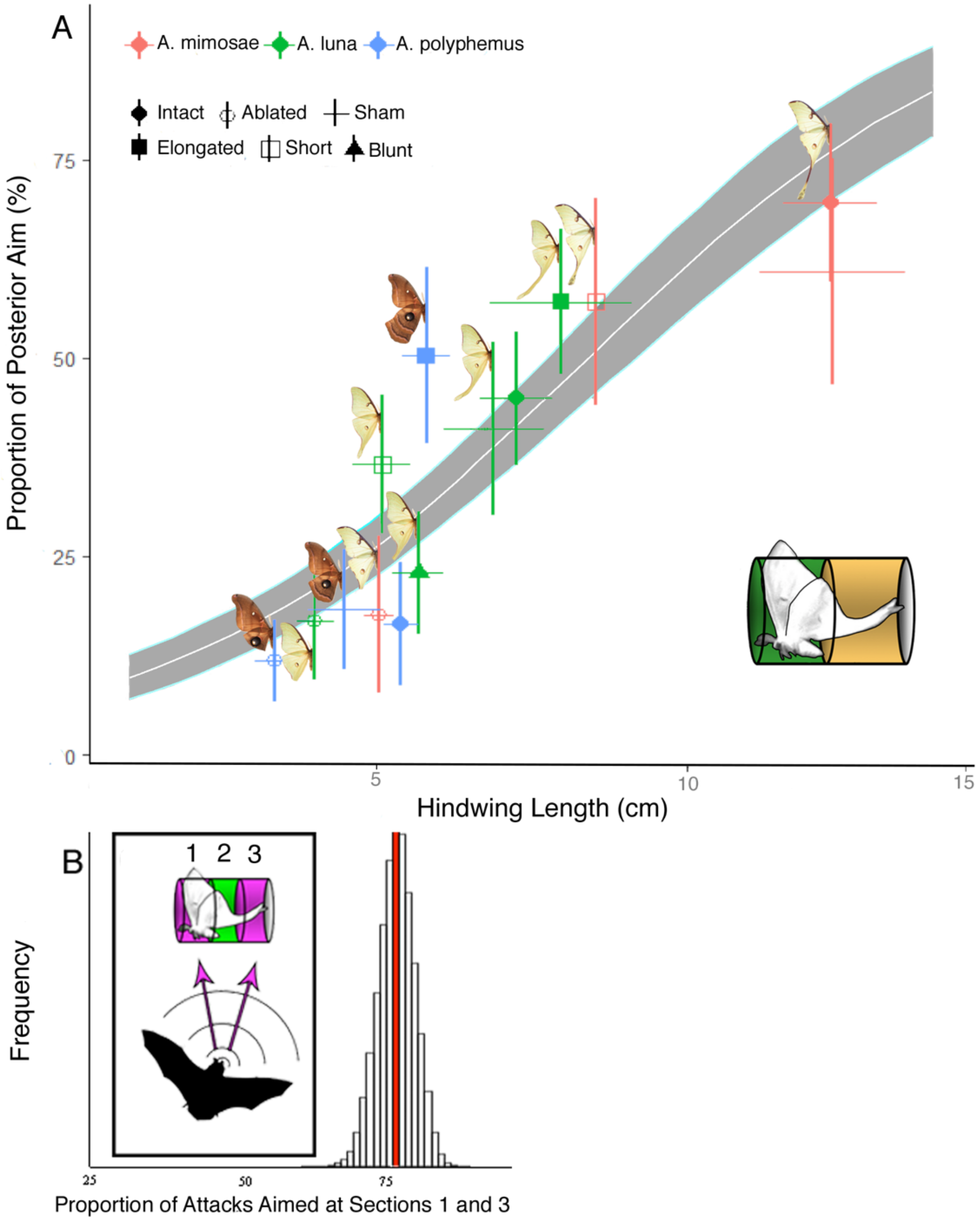
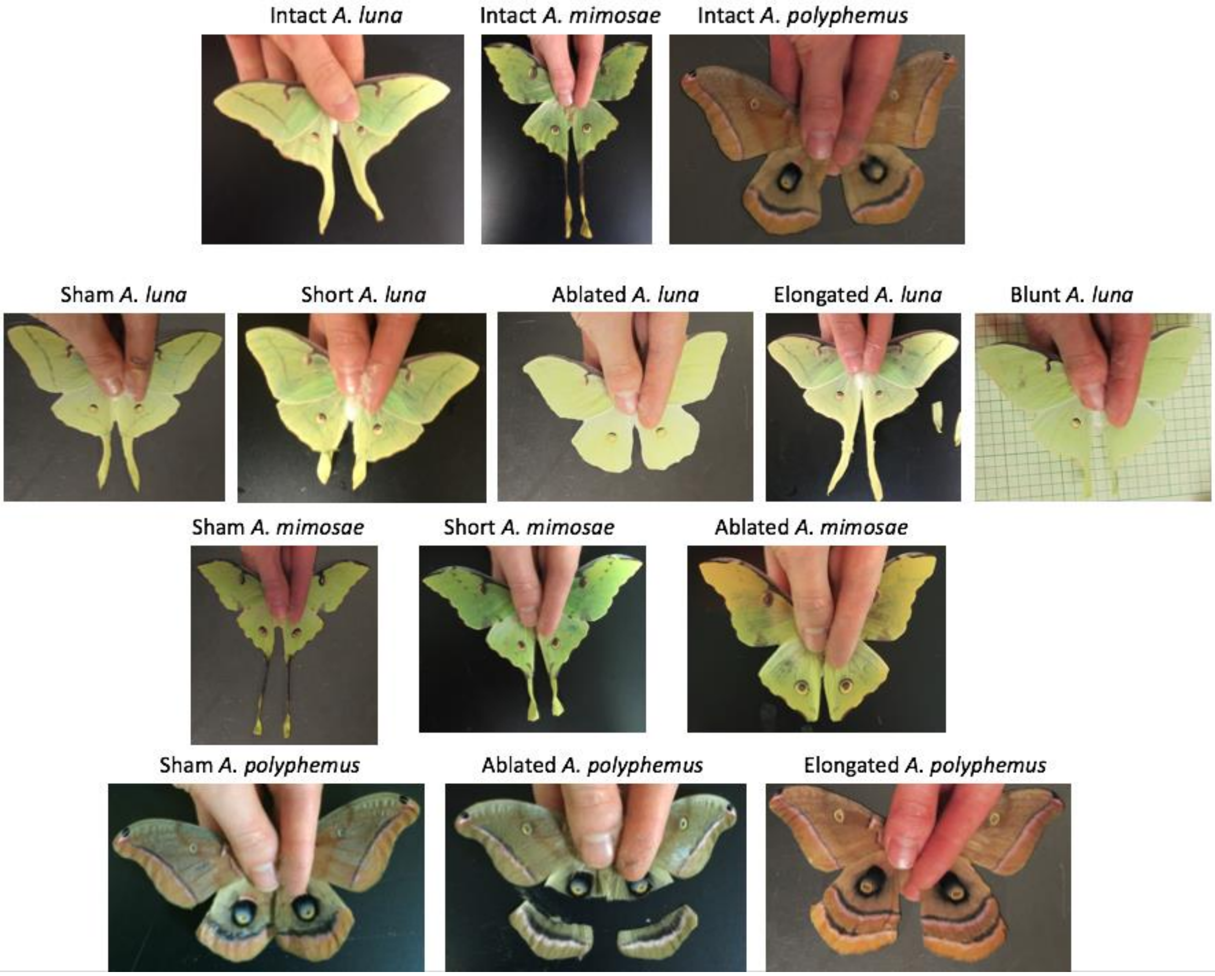


Figure 3. Posterior Aim. 3A. Bats directed an increasing proportion of their attacks at the posterior half of the moth (indicated with the yellow cylinder) as moth hindwing length increased. Results extracted from a Bayesian analysis with bat identity and hunting night included as random intercepts. 3B. Two-target Aim. The enlarged echo sensory illusion predicts that bats will target the hindwing just behind moth abdomen, at the perceived echo center (section 2, highlighted in green, 3C). The multiple target sensory illusion predicts that bats will target either section 1 or section 3 of the moth's body (highlighted in purple, 3C). Bats aimed 75% of their attacks on tailed moths (*A. luna* intact, sham, elongated; *A. mimosae* intact, sham, shortened) at the first and third sections, providing support for the multiple target illusion.

Pictures

Picture 1. “Dodge.” A big brown bat (*Eptesicus fuscus*) echolocating during a feeding.



Picture 2. Moth Treatments. Polyphemus treatments were created by cutting hindwing material just below the eyespot (ablated) and regluing (sham), or by adding hindwing material cut from below another animal's eyespot to the end of an intact animal's hindwing (elongated). Luna and moon moth treatments were created by cutting tail material where it adjoins the hindwing (ablated) and re-gluing the entirety (sham), or just the twisted and cupped end (short). Additional luna treatments were created by cutting the twisted and cupped ends off (blunt) and gluing an entire second tail to the remaining projection (elongated).

Picture 3. Twisted and Cupped Tails are Found in Other Families. Four representative species from four different families (listed above each picture) where elongated and structured hindwing tails have evolved. The dotted line delineates an independent evolution across Order, from Lepidoptera to Neuroptera.

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APPENDIX A

Tables

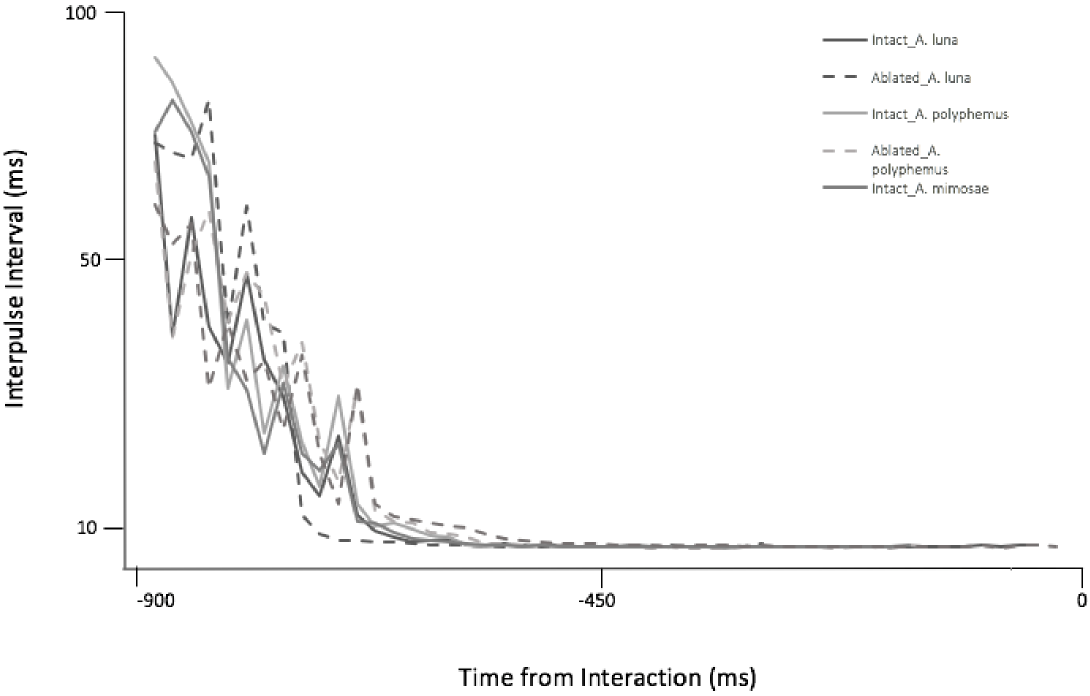
Table A1. Mean Angular Velocity Included is Uninformative to the Model. When including mean angular velocity as a variable in the escape model (Figure 2), we find that it is not a relevant variable to the model (Overlap 0 = TRUE) and does not affect model inference (mean slope of the line is negative, in the opposite direction from the overall escape model slope).

	ean	D	Overlap 0
Mean Angular Velocity	0.107	.126	TRUE

Table A2. Escape Model Slope With Luna and Polyphemus Moths Only is the Same as Aggregate Escape Model Slope. Bayesian models including all moth genera, and luna and polyphemus moths only reveal that moon moths do not drive the mean slope of the line, but are a contributive part of the overall trend.

	Mean	SD	Overlap 0
Luna + Polyphemus	0.169	0.062	FALSE
Aggregate	0.178	0.046	FALSE

Figures



Echolocation results

Figure A1. IPI of Echolocation Call Against Intact and Ablated moths. One representative call against an individual moth from Intact and Ablated treatments of each species demonstrates that IPI does not change between tailed and non-tailed individuals.

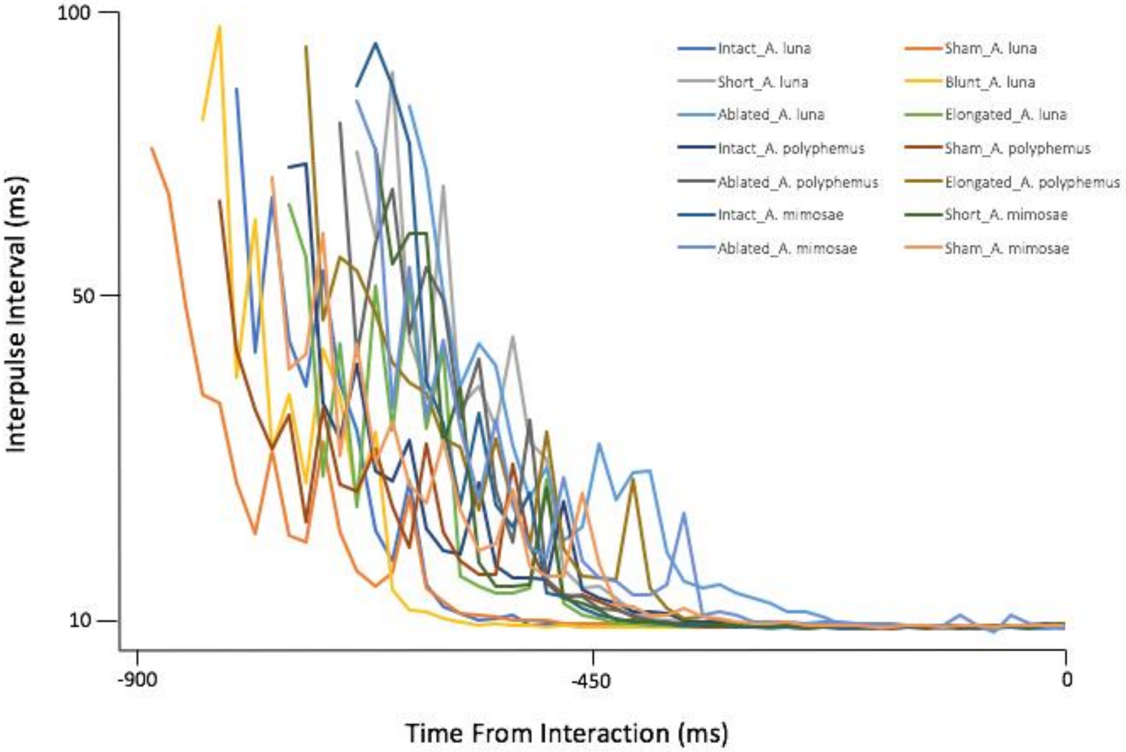


Figure A2. IPI of Echolocation Call Against all Treatments. One representative call against an individual moth from each treatment depicts the same results as our Bayesian model built with logit links: IPI during bat attack is not different based on moth genus or tail length (slope of the line IPI versus tail length (cm) = -0.05±0.04, Overlap 0=TRUE). Buzz duration (slope of buzz duration versus tail length (cm) = -0.04±0.04, Overlap 0=TRUE) and frequency 15dB below frequency at peak amplitude were also not different (slope frequency 15dB below and above versus tail length (cm) = 0.00±0.03, Overlap 0=TRUE).