Light suppresses the acoustically prompted predator-avoidance behaviour in moths

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ABSTRACT

Urbanization leads to increased light exposure of wild animals. Especially nocturnal animals are affected by artificial light, which shifts balances of animals' interactions. Predator-prey interactions, for example, can be shifted either in favour of the prey or the predator under the influence of light. In the interaction between echolocating bats and eared moths, bats often benefit from moths eliciting less last-ditch behaviour in response to close-by attacking bats when exposed to light. In contrast, it is unknown to which extent light also affects moths' negative phonotoaxis, which moths elicit in response to distant bats. To quantify the overall effect of light on both last-ditch behaviour and negative phonotaxis, we counted over several nights the moths caught by two light traps, which were alternatingly equipping with speakers broadcasting ultrasonic simulations of hunting bats. Playbacks did not affect moth counts, indicating that light not only reduces the last-ditch behaviour of moths, but also their negative phonotaxis. The increasing light pollution therefore interferes with different aspects of anti-predator behaviour in moths, and possibly other eared insects. Our study emphasizes the negative effect of lights on insects and the need to further study the underlying mechanism.

KEY WORDS

Artificial light at night (ALAN), predator-prey, bats, Noctuidae, light traps, playback experiment

BACKGROUND

One-fifth of the world's human population cannot see the Milky Way anymore (1), caused by the substantial increase of artificial light at night (ALAN) over the last decades, causing increasing light pollution (2,3). Likewise, also plants and animals are affected by increasing light pollution (4–6). Light pollution can impact a single species' orientation, reproduction or communication (4), but also affects whole communities, for example by shifting the balance of trophic interactions such as predator-prey interactions (7–12).

Echolocating bats preying upon eared moths are a global predator-prey system with important ecological impacts (13–16). Bats and moths are primarily nocturnal and strongly rely on their sense of hearing to communicate, orientate, hunt or defend themselves. When bats search for their food, they emit echolocation calls to probe the environment (17,18). Eared moths are able to hear those calls and to respond with a two-staged anti-predator flight behaviour (19,20). During stage one, moths show negative phonotaxis, i.e. they fly away from the calling bat. Negative phonotaxis is elicited when the bat is still far away and serves the purpose of avoiding detection by the bat. During stage two, moths show last-ditch behaviour such as erratic manoeuvres or diving to the ground. Last-ditch behaviour occurs when the bat is nearby and serves the purpose of avoiding capture by the bat. Whether negative phonotaxis or last-ditch behaviour is elicited depends on the acoustic properties of the bat's echolocation call received at the moth's ear, most importantly received sound pressure level, but also call length and call repetition rate, which provide information about the distance and behaviour of the bat (17). The received sound pressure level of distant bats is fainter than of nearby bats, due to spherical spreading and atmospheric attenuation (21). Despite this predominantly acoustic interaction, both bats and moths are strongly affected by artificially introduced light sources. While some bats may profit from artificial light, for

example by exploiting resulting accumulations of prey animals (22,23), other species are also negatively affected, for example when commuting or distribution to new habitats is interrupted or hindered (24–26). Moths are mainly negatively affected by light. Light strongly attracts moths, which interrupts and reduces their feeding (27,28) and commuting behaviour (29), resulting in ecological consequences such as reduced pollination (30) or population decline (27,31). Light also increases moth's predation risk in two ways. First, moth accumulations around lights attract bats, thus increasing the moth's predation pressure (22,23). Second, light impedes the moths' anti-predator flight behaviour. Several studies that compared the sound-induced anti-predator flight of moths between lit and unlit conditions reported a reduction of anti-predator flight in light. Wakefield et al. (32) specifically studied last-ditch behaviour, showing that only 24% of moths performed power-dives under LED illumination compared to 60% in darkness, i.e. LED-illumination inhibited the last-ditch behaviour in 60% of the moths that reacted in darkness. Similarly, Svensson & Rydell (33) reported a reduction of ~60% within a radius of 1 meter around the light source compared to darkness (where all moths reacted), also mostly noticing last-ditch evasive behaviour. Minnaar et al (34) reported the most extreme effect, showing that the model without light-induced reduction in anti-predator flight behaviour explained best the differences in bat diets between lit and unlit conditions. Another set of studies kept the light exposure constant while manipulating the sound received by the moth, showing that moths still exhibit some degree of anti-predator flight under illumination. Acharya & Fenton (35) compared last-ditch behaviour of eared and deafened moths under illumination, showing that 48% of eared moths exhibited last-ditch behaviour when attacked by bats, whereas deafened moths did not exhibit any erratic flight. Agee & Webb (36) and Treat (37) compared the number of caught moths at light traps with and without ultrasonic stimuli. In

both studies, ultrasound reduced the capture rates at the light trap with ultrasound playback compared to the silent light trap to various degrees depending on stimulus design and moth family. Across different stimulus types, capture rates at the sounding light trap were reduced by 51-86 percentage points compared to the capture rate at the silent trap in a Noctuid species (*Heliothis zea*, (36)), and by 8-49 percentage points for different eared moth families (with a minimum sample sizes of 37 individuals in total, (37)). In summary, while some studies confirm that light has a suppressive effect on the anti-predator flight of moths, ranging from 60-100% suppression when comparing acoustically elicited anti-predator behaviour in dark and lit conditions, other studies confirm that even under light conditions there is a repelling effect of the playbacks, ranging from 8-86 percentage points when comparing attraction to light under ultrasonic and silent conditions. Therefore, the extent of light suppressing anti-predator flight in moths is unclear. Importantly, however, the majority of those studies either focused on (32) or naturally observed (33) only last-ditch behaviour. Even in the studies of Treat (37) and Agee & Webb (36), where the stimuli potentially elicited both types of evasive flight behaviour, last-ditch behaviour was likely dominating the outcome due to the study design. Both studies used directional light- and sound sources which made it likely that moths attracted to the light were always exposed to sufficiently high sound levels that could elicit last-ditch behaviour. Only Minnaar et al. (34) (indirectly) investigated both stages of evasive flight by observing the diet of naturally foraging bats under lit and dark conditions, suggesting that light under these more naturalistic conditions may completely suppress the antipredator flight throughout the natural moth population. Yet, a direct quantification of the overall effect of light on both stages of the anti-predator flight in moths is missing. Here, we designed an experiment to investigate the effects of light on both last-ditch behaviour and negative phonotaxis. Like Agee & Webb and Treat (36,37),

we compared moth captures at two light traps, while alternatingly simulating bat predation pressure via ultrasonic playbacks at one light trap. We combined an omnidirectional light field (attracting moths equally) with a directional sound field. Therefore, sound intensities around the light trap varied and therefore triggered either last-ditch behaviour (on-axis) or negative phonotaxis (off-axis) in proximity to the trap.

We predicted three different outcomes, depending on the effect of light on the two stages of moths' antipredator flight: (1) No moth captures at the ultrasonic light trap, indicating that both stages of sound-elicited antipredator flight is functional and not suppressed by light. (2) Reduced moth capture rates at the ultrasonic light trap, indicating that light partly suppresses sound-elicited anti-predator flight. (3) Equal captures at both light traps, indicating that light completely suppresses both stages of sound-elicited antipredator flight.

METHODS

Setup, study site, moth capture and measurement

We compared the number of caught moths between two light traps, one additionally equipped with a loudspeaker, to examine the effect of light on the evasive flight behaviour of eared moths. We set up two equal light traps (Sylvania, blacklight, F15W/350BL-T8, USA, Fig 1A) at 30 m distance to each other, one at a path in a forest (trap A) and one in the forest itself (trap B), close to the Max Planck Institute for Ornithology, Seewiesen, Germany. Both traps hung freely at ~1.7 m above ground, radiating light at 360° in the horizontal plane (Fig 1A). We collected data over 15 rainless nights between the 19th of July and the 16th of August 2018. Each test night, we alternatingly equipped one of the two traps with two loudspeakers (Ultrasonic Dynamic Speaker ScanSpeak, Avisoft Bioacoustics, Germany)

134 broadcasting an ultrasonic stimulus (see below) to simulate echolocating bats. We fixed both
135 speakers back to back facing into opposite directions and mounted them above one of the
136 light traps at ~2 m above ground, associating each trap for 7-8 nights with the playback. We
137 switched the light of the traps and the acoustic playback on in the evening (between 20:30h
138 and 23:40h) and off the next morning (between 7:00h and 9:40h). After switching off, we
139 emptied the traps each morning and counted all moths of the ear-possessing families
140 Noctuidae, Geometridae, and Sphigindae. We measured the individuals' body length along
141 the middorsal line (from the head to the end of the abdomen), to correct for the fact that
142 larger moths are more sensitive (38,39). For those individuals whose body length we could
143 not measure (e.g. due to missing abdomen, N = 137, 15.5%) we either used the mean value
144 of the same species or, if this was not possible (N = 1), the mean value of the family.
145
146 **Ultrasonic playback stimulus design and evaluation**
147 We simulated predation pressure by echolocating bats by playing an ultrasonic stimulus
148 consisting of repeated pure tones. The stimulus was designed based on the acoustic
149 properties of bat echolocation calls (call frequency, duration, and interval) and the hearing
150 system of moths. Pulse frequency was 35 kHz, matching most moths' best hearing threshold
151 between 20-50 kHz (Noctuidae: (39,40); Erebidae: (41); Pyralidae: (42); Geometridae:
152 (43,44); Sphingidae/Drepanidae: (40)). Pulse duration was 10 ms including 2 ms linear rise
153 and fall time, i.e., corresponding to the longer calls of European open space bats (45,46), to
154 optimize detection by moths and information transfer about bat distance (47). The
155 interpulse interval was 100 ms, matching the call interval of bats' echolocation calls in their
156 search phase (60 - 200 ms, (45,48)). On-axis sound pressure level was 98 dB SPL re. 20 µPa
157 RMS at 1 m distance (see below for a detailed description of the sound field). This stimulus

158 was presented continuously in a loop throughout the night via the loudspeakers using
159 Avisoft-RECORDER software (Avisoft Bioacoustics, Germany), a sound card (Avisoft
160 UltraSoundGate 116, Avisoft Bioacoustics) and a laptop (DELL Latitude E6540, Dell
161 Technologies Inc., USA).
162 To validate the effect of the stimulus in darkness, without the potential suppressing
163 influence of light, we exposed free-flying moths in a dark flight room (5.3 m x 3.5 x 3 m^3) to
164 the stimulus. We caught moths at trap A over the course of four nights and tested them
165 within 30 hours after capture. We placed moths on the ground of the flight room and
166 recorded the flight paths of upwards flying moths with an IR-sensitive camera (Sony HDR-
167 CX560, Sony) under IR illumination (850 nm, Mini IR Illuminator TV6700, ABUS Security-
168 Center). Using the same audio equipment as described above, we presented the stimulus by
169 manually triggering when a moth flew in front of the speaker. The moth's distance to the
170 speaker at stimulus onset was about 1-2 m. We categorized the recorded flight paths as
171 "reaction", when the flight direction, level of erraticness, or both changed with stimulus
172 onset (for examples see Supplement Information); as "no reaction", when we did not
173 observe those changes; or as "ambiguous", if we could not assign the flight path to one of
174 the other categories. In total, we evaluated 32 flight paths with ten moths (31.2 %) showing
175 a reaction, twelve moths (37.5%) not showing a reaction, and eleven moths (34.3%) were
176 categorized as "ambiguous".
177
178 **Overlap of sound and light field**
179 The range and geometry of the presented sound and light fields differed. While the light was
180 emitted omnidirectional in the horizontal plane, the sound field was directional (Fig. 1). We
181 estimated the biologically effective range for the attraction by light and the biologically

182 relevant sound fields for triggering evasive flight behaviour based on literature values and
183 own measurements.
184 Light traps can attract released moths from up to 80 m distance, yet recapture rates
185 dramatically decrease beyond 15 m, and additionally depend on family (49,50). Family-
186 specific modelled 5%-recapture rates are 10 ± 6 m (mean ± SEM) for Noctuidae and 23 ±
187 12 m for Geometridae (49). Note, however, that these data were obtained with a different
188 light source (6W actinic vs. 15W blacklight in our case), and that the radius of attraction to
189 light is not necessarily equivalent to the radius over which light interferes with anti-predator
190 behaviour. Yet, we used these family-specific values as first estimates of the biological
191 relevant distances for the attraction of moths to our light trap (Fig. 1B, dashed lines).
192 To estimate the effect of the playback, we measured the playback level of the loudspeaker
193 from 0° on-axis to 90° off-axis in steps of 5° (for details about calculations see Supplement
194 Information). On-axis source level was 97 dB SPL re. 20 µPa RMS @ 1 m distance, i.e. within
195 the lower range of natural bat call levels in the field (100-120 dB peSPL @ 1 m (48), with
196 corresponding RMS-SPL values being ~3-7 dB lower than the peSPL values (51,52)). Playback
197 source level was reduced with increasing off-axis angle by up to ~30 dB at 45°, resulting in a
198 minimum playback level of 70 dB SPL RMS @ 1m. We then calculated the angle-dependent
199 distances to the loudspeaker where the playback would reach biologically relevant levels of
200 60 and 80 dB SPL RMS. We chose 60 and 80 dB SPL as approximate thresholds for eliciting
201 negative phonotaxis and last-ditch behaviour, respectively, based on several lines of
202 evidence. Triggering of negative phonotaxis and last-ditch behaviour in moths is supposed to
203 be correlated with the activity of moths' auditory receptor neurons A1 and A2, respectively
204 (47,53,54). The neuronal thresholds of these neurons vary with frequency and species
205 (39,47,53,55–57) with A1 being generally about 20 dB more sensitive than A2 (39,53,58). A1

best thresholds range from ~35-55 dB SPL at the position of the moth, and A2 best thresholds range from ~52-72 dB SPL (20,39,47,53,55,56). Where known, behavioural thresholds in moths are often ~10 dB higher than neuronal ones (reviewed in (52)). Indeed, our own data indicate that sound pulses of ~80 dB SPL elicit last-ditch behaviour (59), which is 8-28 dB above known A2 thresholds (20,39,47,53,55,56). As no behavioural data exists for the threshold of negative phonotaxis, we chose 60 dB SPL, i.e., 20 dB below the threshold for last-ditch behaviour, matching the difference between A1 and A2 thresholds. We calculated the distance-isolines for 60 and 80 dB SPL, which varied with the angle around the loudspeaker, ranging from 3.6-14.6 m and 0-5.6 m, respectively (Fig. 1B).

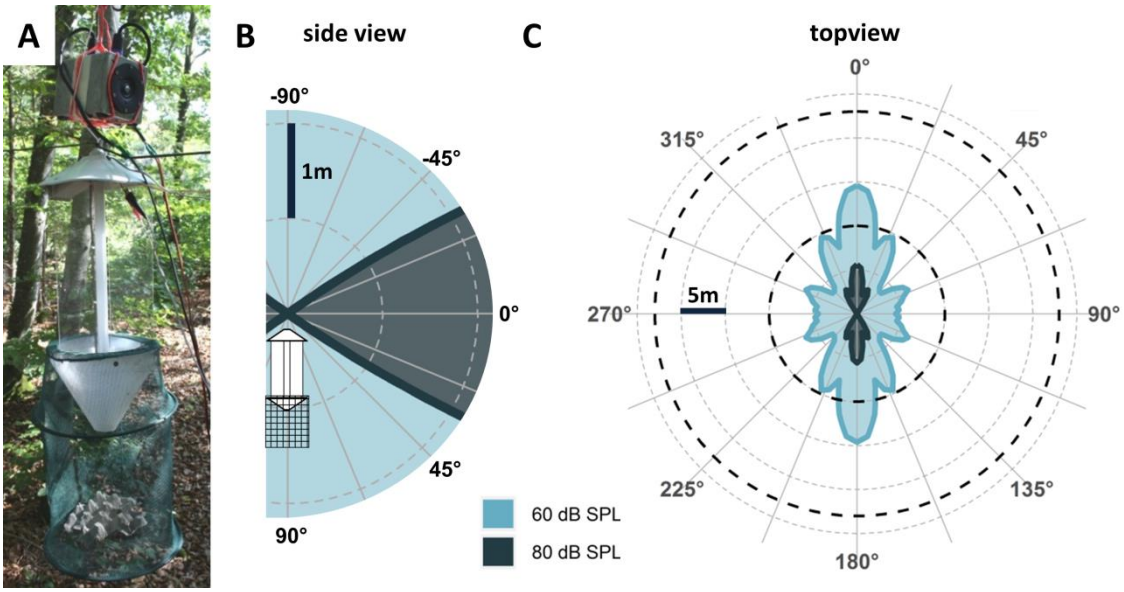

Figure 1: (A) Experimental setup. One of the light trap with two loudspeakers attached above the trap, which broadcast the acoustic stimulus in opposite directions. **(B) Side view of the biological effective sound field around the light trap with attached loudspeakers.** Coloured areas indicate areas with minimum sound levels of 60 and 80 dB SPL re. 20 µPa, which are biological relevant acoustic thresholds for eliciting negative phonotaxis and last-ditch behaviour, respectively, in eared moths. Schematic indicates position and dimenstion of the light trap. **(C) Top view of the biological effective sound field (coloured areas) and light field (dashed lines)**. Dashed lines indicate the distance of 5% recapture rate for noctuid (10 m) and geometrid (23 m) moths, respectively (49), as an indicator of the maximum range of light attraction.

228 **Statistical analysis**

229 To test for an effect of light on the moths' negative phonotaxis, we fitted linear mixed-
230 effects models to the moth count data as a function of the fixed effects *playback*, *trap*, *moth*
231 *family*, and *moth body length*, the random factor *date* (to account for repeated measures),
232 and the interactions of *playback* and *moth family*, and *playback* and *moth body length*.
233 Count data were log-transformed to approximate a normal distribution. Even though normal
234 distribution was not achieved, we selected the log-transformed model over the alternative
235 Poisson-model, as this showed some signs of overdispersion (dispersion factor = 1.4) making
236 it less reliable than the log-transformed Gaussian-model with an incomplete normal
237 distribution (60). We defined the moth family Noctuidae as intercept, as it had the largest
238 sample size and thus was the most reliable reference. To test which factors significantly
239 contributed to the model fit, we conducted backward model reduction. We compared
240 models with likelihood ratio tests using a chi-squared statistic to find the minimal adequate
241 model. All statistical analyses were conducted in R version 3.3.2 (R Foundation for Statistical
242 Computing, Vienna, Austria) using the packages "lme4"(61), "lmerTest"(62), and "blmeco"
243 (63).

244
245
246

247 **RESULTS**

248 We caught a total of 871 moths over 15 experimental nights (range: 7-115 moths per trap
249 and night, Fig. 2). The minimal adequate model included *playback*, *family* and *size* as fixed
250 and *date* as random factors. Capture success varied between moth families (likelihood ratio
251 test for factor *family*, $\chi^2 = 62.814$, d.f. = 3, $p < 0.001$). The vast majority of 81.2% of the
252 moths belonged to the family Noctuidae, the remaining 18.8 % were composed of

Geometridae (11.4%), Erebidae (6.9%), and Sphingidae (0.5%). Moths of these four families possess ears, except for Sphingidae where ears might be a derived structure as they are only found in two subtribes (64–66). We caught more small than large moths (likelihood ratio test for factor *size*, $\chi^2 = 89.856$, d.f. = 5, $p < 0.001$). Although capture rates seemed to differ between traps (total capture of 506 (trap A) vs. 365 (trap B), Fig 2A), *trap* was not a significant factor of the minimal adequate model (likelihood ratio test, $\chi^2 = 0.488$, d.f. = 1, $p = 0.484$).

Our playback treatment had no effect on the number of caught moths, i.e. the number of caught moths did not differ between nights with and without playback (Fig. 2A, likelihood ratio test of factor *playback*, $\chi^2 = 1.084$, d.f. = 1, $p = 0.297$). There was also no significant effect of the interactions between *moth size* and *playback* and of *moth family* and *playback* on the model fit (likelihood ration tests, $\chi^2 = 3.159$, d.f. = 3, $p = 0.367$ and $\chi^2 = 1.328$, d.f. = 3, $p = 0.722$, respectively).

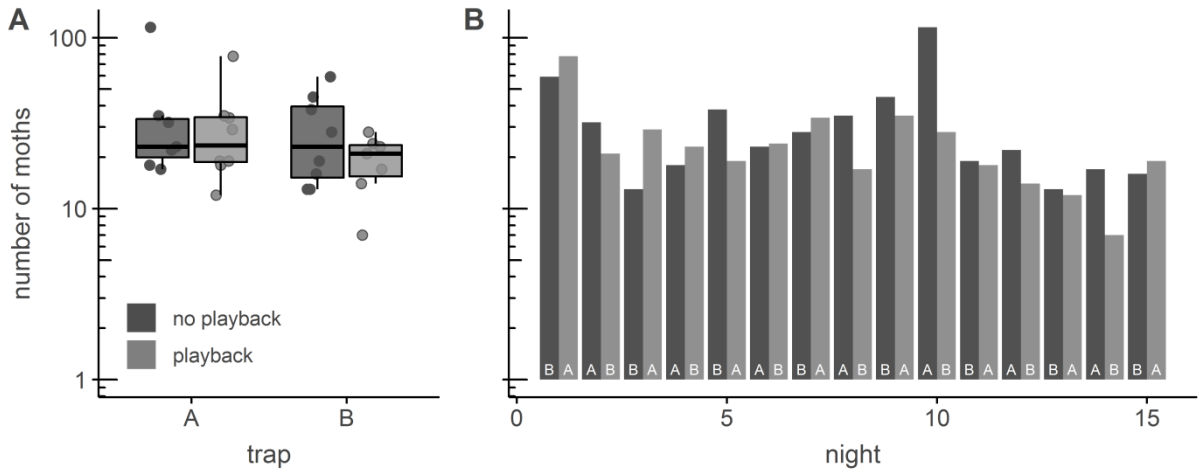

Figure 2: Number of caught moths per night and playback treatment. **(A) Number of caught moths at both light traps without and with playback.** Boxplots show median, quartiles and whiskers (up to 1.5 x inter-quartile range) of the daily counts (dots). **(B) Daily counts of caught moths per night and trap for all 15 nights.** White letters at the base of the bars indicate the trap.

274 **DISCUSSION**

275 Echolocating bats and eared insects are a textbook example of predator-prey interactions,
276 which is based on acoustic information (20). Increasing artificial light at night (ALAN) (2,3),
277 however, severely impacts both bats and moths (e.g. (23,24,28)), with potential cascading
278 effects on their predator-prey-interactions, population dynamics and ecosystems (11,34).
279 Light reduces the acoustically triggered last-ditch behaviour of eared moths, making them
280 more vulnerable to close-by attacking bats. In contrast, it is less clear whether light also
281 reduces negative phonotaxis in eared moths, which serves as their first line of defence
282 against distant echolocating bats. To better understand how artificial light at night affects
283 the overall capability of predator avoidance in eared moths, we compared moth captures at
284 two light traps. One trap was "silent", while the other trap broadcast bat-like ultrasonic
285 stimuli that trigger last-ditch behaviour as well as negative phonotaxis under dark
286 conditions. We caught the same number of moths at both traps. Thus, the presented
287 playback did not repel the moths, suggesting that the light suppressed both anti-predator
288 behaviours, negative phonotaxis and last-ditch behaviour.

289 In contrast to our results, Treat (37) and Agee & Webb (36) both showed a repelling effect of
290 their playbacks on moth capture rates at the ultrasonic trap. We deem differences in
291 stimulus design and habituation effects of the moths unlikely to explain these differences.
292 Treat (37) and Agee & Webb (36) broadcast a variety of different stimuli varying in pulse
293 rate, frequency, pulse duration, and SPLs (ranges: pulse rate:0.7-155 pulses/s; frequency:
294 12.5-200 kHz; pulse duration: 2-10ms; SPL: ~60-100 dB SPL @ 1 m distance), which all
295 elicited evasive flight to various degrees in eared moths. As our stimulus had acoustic
296 properties within this range and elicited evasive flight in unlit conditions, we doubt that
297 differences in the stimuli can explain the difference in capture rates. Habituation to the

298 ultrasound could have affected individuals that flew close to the light traps for extended
299 time periods. It is more likely, however, that most caught individuals randomly encountered
300 and approached the traps over larger distances and thus did not perceive our presented
301 stimulus continuously. Likewise, Agee & Webb (36)also presented their ultrasonic stimuli
302 over the course of a whole night and were able to detect a repelling effect of their
303 playbacks.
304 We suggest that major differences in the geometry and overlap of light- and sound-fields
305 could explain these contrasting results. In the setups of Treat (37) and Agee & Webb (36),
306 sound and light fields were almost overlapping. Before entering the light traps in these
307 setups, approaching moths had to pass high sound pressure levels, which were sufficiently
308 high to potentially elicit last-ditch behaviour. Both studies indeed caught fewer moths in the
309 ultrasonic trap compared to the silent trap, suggesting that the playback elicited still some
310 anti-predator flight (likely last-ditch behaviour) under these light and sound conditions.
311 Specifically, for stimuli similar to ours, the capture rate for noctuid moths was 35% for a
312 37.5 kHz pulsed tone stimulus vs. 65% at the silent trap (37), while Agee & Webb (36)
313 reported ~15% capture rate for 30 kHz pulsed tones vs. 85% at the silent trap for two species
314 of the families Noctuidae and Pyralidae. In contrast, our setup combined omnidirectional
315 light fields with directional sound fields, which exposed the moths to different direction-
316 dependent sound pressure levels (SPLs) while approaching the light. Moths approaching the
317 trap on-axis were exposed to first low and then increasingly higher SPLs that should first
318 elicit negative phonotaxis and later last-ditch behaviour. In contrast, moths approaching the
319 trap off-axis were exposed only to lower SPLs that can only elicit negative phonotaxis. As our
320 capture rates did not differ between the light traps, i.e., indicating no repelling effect of the
321 playback on moth flight, we suggest that the light strongly reduced the negative phonotaxis

322 of eared moths. Even if the moths still exhibited some degree of last-ditch behaviour close to
323 the trap (as shown by Treat and Agee & Webb, (36,37), these last-ditch manoeuvres might
324 bring the moth into a position off-axis to the loudspeaker, either to the sides or below the
325 loudspeaker, where the SPL is lower. Due to the lower SPL, no further last-ditch evasive
326 flight is elicited, while the light keeps attracting the moth into the trap. Our results are in line
327 with Minnaar et al. (34), who found that a model assuming 0% efficiency of escape
328 behaviour in moths best explained bats' diet under lit conditions. We therefore suggest that
329 light not only suppresses last-ditch behaviour, as previously shown but also negative
330 phonotaxis.
331 In summary, our results underline the strong effect of (artificial) light on eared moths,
332 providing an additional explanation for shifts in predator-prey interaction between bats and
333 moths (11,12,34). With negative phonotaxis also being suppressed by light, additionally to
334 last-ditch behaviour, moths are not just unable to escape predators, but also to avoid them.
335 Similarly, fish are attracted to lit areas, where they are "trapped" and predated upon by
336 seals (9) and other fish (67). Our results emphasize the need for understanding the
337 mechanisms underlying animals' attraction to light and other effects of light on animals'
338 behaviour, such as predator avoidance. This is particularly important given the increasing
339 light pollution and the general decline of insect populations. Only by understanding
340 underlying mechanisms, we can apply efficient conservation measures.

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Competing interests

We have no competing interests.

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Author contributions

TH and HRG conceived of and designed the study.

TH collected and analysed the data.

TH and HRG wrote the manuscript.

All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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