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Auditory predator cues decrease herbivore survival and plant damage

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Abstract

The high fitness cost of predation selects prey capable of detecting risk cues and responding in ways that reduce their vulnerability. While the impacts of auditory predator cues have been extensively researched in vertebrate prey, much less is known about invertebrate species' responses and their potential to affect the wider food web. We exposed larvae of *Spodoptera exigua*, a slow-moving and vulnerable herbivore hunted by aerial predators, to recordings of wasp buzzing (risk cue), mosquito buzzing (no-risk cue), or a no-sound control in both laboratory and field settings. In the laboratory, wasp buzzing (but not mosquito buzzing) reduced survival relative to the control; there was, however, no effect on time to or weight at pupation in survivors. In the field, wasp buzzing reduced caterpillar herbivory and increased plant biomass relative to the control treatment. In contrast, mosquito buzzing reduced herbivory less than wasp buzzing and had no effect on plant biomass. The fact that wasp cues evoked strong responses in both experiments, while mosquito buzzing generally did not, indicates that caterpillars were responding to predation risk rather than sound per se. Such auditory cues may have an important but largely unappreciated impacts on terrestrial invertebrate herbivores and their host plants.

KEYWORDS
auditory cue, herbivory, nonconsumptive effects, predation

INTRODUCTION

Predator–prey interactions are the linchpin of food webs and a central focus of community ecology. The high fitness costs of even unsuccessful predator attacks select prey capable of detecting, avoiding, and deterring predators. The resulting changes in behavior and/or physiology can yield risk-induced trait responses ("RITRs," sensu Peacor et al., 2020) and nonconsumptive effects (NCEs) in prey. Despite debate regarding the ability of predation risk to generally elicit population-level responses in prey and prey resources (Sheriff et al., 2020), it is clear that such impacts can occur under appropriate conditions (Allen et al., 2022; Alvarez & Peckarsky, 2014).

Although prey can employ an array of sensory modalities to detect predators, research into RITRs and NCEs has been dominated by work on chemical cues in aquatic systems (Draper & Weissburg, 2019; Weissburg et al., 2014).

This bias, while reflective of the relative ease with which researchers can manipulate various aspects of cue exposure using caged predators and/or flow-through systems, belies the importance of auditory cues in terrestrial predator–prey interactions (Hettena et al., 2014). Research on this modality has focused primarily on vertebrate taxa. Both mountain lions and smaller vertebrate predators reduced activity in and/or avoided areas where recordings of human conversation were broadcast, leading to increases in small mammal foraging (Suraci et al., 2019). Similar behavioral changes in response to avian predator calls have been documented in multiple bird species (MacLean & Bonter, 2013). These cues can also affect fitness: songbirds exposed to auditory predator cues laid fewer eggs and fledged fewer young, for instance, while those exposed to control sounds were unaffected (Allen et al., 2022; Zanette et al., 2011).

Despite the importance of auditory predator cues for vertebrate prey and the knowledge that sounds can be a stressor for insects, there has been little research into how and whether such information is used by invertebrates (Barton et al., 2018). With the notable exception of bat–insect interactions (reviewed in Pollack, 2016), insect responses to auditory predator cues have received scant attention (Yack et al., 2020). A recent review of insect responses to predation risk, for instance, listed multiple experiments manipulating visual and/or chemical predator cues but did not mention sound as a modality for prey threat assessment (Hermann & Landis, 2017). Studies that have explored the ability of insects to detect predators using vibrational cues have largely focused on plant- or substrate-borne vibrations rather than airborne sound (Castellanos & Barbosa, 2006; Gish, 2021; Roberts, 2017). This gap is surprising because insects employ sound for an array of purposes (Low et al., 2021; Mason & Pollack, 2016) and laboratory-based work has documented predator-specific responses to auditory cues in multiple species (Breviglieri & Romero, 2019; Lee et al., 2021; Tautz & Markl, 1978; Taylor & Yack, 2019).

Insects are the dominant herbivores in many ecosystems (Laws et al., 2018) and are of increasing ecological importance given the collapsing populations of large vertebrate herbivores (Ripple et al., 2015). Larval lepidopterans ("caterpillars") feed on a wide range of plant species and are commonly preyed upon by social wasps (Lichtenberg & Lichtenberg, 2003; Stamp & Bowers, 1988). These slow-moving and vulnerable prey "hear" their aerial predators using lateral hairs (Tautz & Markl, 1978) whose maximum sensitivity corresponds to wasp buzzing (Tautz, 1977). Caterpillars with intact filiform hairs respond to wasps more than 50 body lengths away from them; those whose hairs have been experimentally removed do not respond to, or apparently even notice, wasps until physically attacked (Tautz & Markl, 1978). Several studies have documented wasp-induced changes in caterpillar behavior, feeding, and survival (e.g., Baranowski & Preisser, 2018; Johnson et al., 2007; Stamp, 1997) and one article found similar responses to the buzzing of nonpredatory honeybees (Tautz & Rostás, 2008). Because these experiments used free-flying insects to generate risk, however, responses to auditory cues cannot be separated from those caused by visual and chemical stimuli.

We conducted experiments assessing the effect of auditory predator cues on caterpillar survival in the laboratory and herbivory in the field. Larvae of our model herbivore, the noctuid moth *Spodoptera exigua* ("*Spodoptera*"), are heavily preyed upon by social wasps (e.g., Southon et al., 2019) and larval Noctuidae respond strongly to wasp buzzing (Tautz, 1977; Tautz & Markl, 1978). Exposing *Spodoptera* to recordings of wasp buzzing, a nonpredatory sound of similar volume, and a no-sound control removes confounding visual and/or chemical cues while allowing us to separate the effect of predator risk from that of sound per se. Our results suggest that RITRs/NCEs stemming from auditory predator cues may have an important, but largely unappreciated, impact on herbivores and the damage they inflict.

METHODS

Laboratory experiment

The laboratory experiment was conducted at the University of Rhode Island (Kingston, RI, USA) in spring 2021. We purchased *Spodoptera* eggs and diet (Frontier Agricultural Sciences, Newark, DE, USA) and reared two generations prior to the experiment. Larvae were reared en masse on ~1 L of diet within aluminum pans and adults were allowed to emerge and breed in cardboard boxes with cheesecloth coverings.

The experiment started at the beginning of the second *Spodoptera* generation. Because of the high mortality rate of early instar larvae, we chose not to work with individual neonates; instead we raised five neonate larvae together in a rearing cup. Five randomly selected neonates were removed from the rearing container, weighed as a five-larvae group, and transferred to a single 350-mL clear polypropylene deli cup containing 25 g of diet. This process was repeated in 36 cups (five larvae per cup, 180 larvae in total). Each of the 36 cups (= replicates) was individually placed in a 20 cm × 20 cm × 30 cm Styrofoam cooler that contained a NiZHi TT-028 MP3 player speaker (Shenzhen Powerunion Technology Co., Shenzhen, Guangdong, China). Each cooler was lit using a low-heat flexible LED lighting strip (My Beauty

Light Inc., Kassel, Germany) from 8 a.m. to 8 p.m. (12 h:12 h, light:dark cycle) each day.

Once all cups had been placed in their Styrofoam coolers, each cup-cooler combination was randomly assigned to one of three auditory risk treatments: a no-sound control, recorded buzzing of a nonpredatory flying insect (*Aedes* sp., mosquito), or recorded buzzing of a predatory flying insect (*Mischocyttarus* sp., caterpillar-hunting paper wasp). The mosquito and wasp sound files were recorded from free-flying insects and generously provided by C. Breviglieri and G. Romero; the recordings had been used previously to assess the behavioral responses of both *Hylesia nigricans* (Breviglieri & Romero, 2019) and *Danaus plexippus* (Lee et al., 2021) caterpillars to auditory cues. Although flies and wasps beat their wings at different frequencies (*Aedes* sp. at 614 ± 14 SD Hz versus *Mischocyttarus* sp. at 188 ± 2 SD Hz in our recordings; Breviglieri & Romero, 2019), we played both sound files at similar volumes: 8 dB more than ambient, measured using a BAFX 3370 decibel meter. This was the highest possible volume before sound bleed-over occurred, allowing us to maximize the observed effect of the treatments. Once the Styrofoam cooler top was in place, each cup was isolated auditorily from surrounding replicates. A decibel meter placed in one cooler registered no increase in sound when recordings were played in an adjacent one, and we were unable to detect any change in table-borne vibrations when the within-cooler speaker was playing. Each sound file was played on a 2-s on, 6-s off continuous loop for 12 h (8 a.m. to 8 p.m.) each day. This frequency of disturbance was consistent with prior work that elicited antipredator responses in *D. plexippus* caterpillars (Lee et al., 2021). In the no-sound control, a recording of silence (taken in an empty room) was played on a similar 2 s:6 s loop to control for the presence of a live speaker (appearance, heat generation, etc.); temperature probes placed in the coolers found no between-treatment differences in within-cooler temperature.

Each cooler-cup combination was checked daily for pupae; each pupa was removed, weighed, and the pupation date recorded. Once all larvae had pupated in a cup, we weighed the remaining diet; all cups contained at least 8 g of diet (approximately one-third of the original amount), indicating that larvae had not run out of food during the experiment. Once all larvae had either pupated or died, we calculated the percentage survival to pupation, mean pupal weight, and mean days to pupation for each replicate.

We used generalized linear models (normal distribution with link identity function) to analyze data on pupal weight, and time to pupation; survival was analyzed using a nominal logistic model. The models included treatment (control, mosquito buzzing, wasp buzzing) as a fixed effect and initial larval weight as a covariate. Tukey's honestly significant difference (HSD) test was used for pairwise comparisons between treatments. All data were analyzed using JMP 9.0.0 software (SAS, 2010).

Field experiment

The field experiment was conducted at East Farm (Kingston, RI, USA), an agricultural research facility managed by the University of Rhode Island, in summer 2021. We purchased tomato seeds (*Solanum lycopersicon* cv. Washington Cherry; David's Garden Seeds, Poteet TX, USA) and grew them in a controlled-temperature ($26 \pm 2°C$, $60\% \pm 10\%$ relative humidity [RH]) greenhouse with ambient light in flats filled with a 10:5:1 ratio (by volume) mixture of peat moss, vermiculite, and organic fertilizer. At 2 weeks after germination we transplanted 200 seedlings into individual 1-L pots. Once the plants had reached ~0.7 m in height we transferred 72 similarly sized plants into the field for use in the experiment.

After the tomato plants were transferred into the field, we placed pairs of waterproof outdoor omnidirectional 20 W speakers (Pohopa Inc., Shenzhen, Guangdong, China) 5 m from each other in a nine-column by two-row array (Appendix S1). Each pair consisted of a primary speaker connected to a portable 8GB MP3 player (Victure Inc., Shenzhen, Guangdong, China) and a secondary speaker connected via Bluetooth to the primary speaker (1° and 2°, respectively, as shown in Appendix S1). The speakers and accompanying MP3 players were covered with lightweight plastic trash bags to protect against heavy rain. Four tomato plants were positioned around each speaker at a 0.3 m distance from it, corresponding to the approximate distance of larval detection of buzzing (Tautz & Markl, 1978). Each plant was enclosed individually in a wire-mesh cage (1 m high by 0.3 m diameter) that was covered with a mesh bag (Agribon-15, Johnny's Selected Seeds, Waterville, ME, USA; 90% light transmission) to exclude flying insects. Each speaker and the four surrounding plants were considered a replicate (Appendix S1, solid-line rectangles); data from the four plants were averaged to generate a mean response. The two paired speakers, each with four tomato plants surrounding them, constituted a column (Appendix S1, dotted-line rectangles) in the experimental design. The two replicates in a column were assigned to one of the three treatments detailed below. A block contained one column from each treatment, and there were three blocks in the experiment (six replicates per treatment).

The three treatments were a no-sound control, a recording of the wingbeats ("buzzing") of a nonpredatory insect (*Aedes* sp.), or a recording of the buzzing of a predatory insect (*Mischocyttarus* sp.). These sound files were the same as those used in the laboratory experiment. The volume was adjusted to ensure that both sound recordings produced decibel levels at the four within-replicate tomato plants similar to those produced by a wasp flying within 5 cm of a caterpillar. A decibel meter was used to measure sound transmission both within and between replicates. Sound transmission from the speaker to within-replicate tomato plants was measured at a level of 8 dB more than ambient, while sound transmission from the same speaker to a tomato plant in an adjacent replicate was measured at <1 dB more than ambient. Each sound file was played on a 1-min on, 10-min off continuous loop for 12 h (8 a.m. to 8 p.m.) each day. This reduced frequency of disturbance (compared with the laboratory experiment) was chosen to provide a more field-realistic exposure level and reduce the chances of larvae becoming habituated to the treatment. In the no-sound control, a recording of silence (taken in an empty room) was played on a similar 1 min:10 min loop to control for the presence of a live speaker. This disturbance frequency reflected the results of a pilot experiment conducted in the previous summer that found hymenopterans (bees and wasps) on or within 5 cm of a flowering tomato plant for 9% of the time (8/90 observations; mean 48.8 s/visit). At the end of each day, the speakers and MP3 players were returned to the laboratory and recharged before being deployed the following day. Because a pilot experiment testing the effect of sound on plant growth in the absence of herbivores found no effect of wasp buzzing on final plant biomass, we did not include treatments assessing how the stimulus (no sound/mosquito buzzing/wasp buzzing) affected plant growth without herbivores.

Shortly before the start of the experiment, we purchased *Spodoptera* eggs (Frontier Agricultural Sciences, Newark, DE, USA). These eggs were attached to wax paper onto which females had oviposited and were timed to hatch within 1 day of arrival. Immediately after receiving them, we used a paper punch to cut 0.5 cm diameter circles of paper from egg-covered areas. Each disk contained 96 ± 5 SE intact eggs and was taken from a single egg mass; *Spodoptera* egg masses in the field contain 50–150 eggs (Wilson, 1934). The following morning, we removed the mesh bag from each plant and determined stem diameter at ground level, height, and the number of fully extended leaves. We then used a safety pin to attach a single paper disk to the underside of an interior leaf of each plant. The mesh bag surrounding each plant was returned and the experiment began. The following day we checked and found neonates on all plants except for two where the paper disk was missing and had to be replaced.

The experiment continued for 3 weeks, at which point all *Spodoptera* larvae had either pupated or died; we did not census within-experiment larval densities because *Spodoptera* larvae are cryptic and difficult to locate repeatedly without damaging the plant. We cut each plant off at ground level and bagged the aboveground biomass before digging up the root ball and returning both to the laboratory. The fruit and all fully expanded leaves on each plant were removed and each leaf was classified as damaged (foliar tissue loss characteristic with *Spodoptera* herbivory) or undamaged (either no damage or damage inconsistent with *Spodoptera*). After the leaf classification was complete, the aboveground biomass (excluding fruits) was dried for 48 h at 60°C and weighed to the nearest 0.01 g. We excluded fruits from the aboveground biomass calculations because we observed that older fruits dehydrated and decayed quickly on the vine. After the root ball was washed clean and patted dry, it was similarly dried and weighed. It took 4 days for all 72 plants to be harvested; we harvested equal numbers of plants per treatment each day and recorded the harvest date as a covariate.

We used a general linear model (normal distribution with link identity function) to analyze data on the percentage of leaves damaged, fruit number, aboveground plant biomass, belowground plant biomass, and total plant biomass. The models included treatment (control, mosquito buzzing, wasp buzzing) as a fixed effect and block, initial number of leaves, initial stem diameter, column, and harvest date as covariates. All data were analyzed using JMP 9.0.0 software (SAS, 2010).

RESULTS

Laboratory experiment

There were significant treatment-level differences in *Spodoptera* survival ($F_{2,32} = 5.89$, $p = 0.007$). Only 70% of larvae in the wasp treatment pupated, versus 85% and 90% in the mosquito buzzing and control treatments, respectively (Figure 1A). Among larvae that survived to pupation, there were no significant differences in either time to pupation ($\chi^2 = 3.76$, $p = 0.152$; Figure 1B) or weight at pupation ($\chi^2 = 4.76$, $p = 0.093$; Figure 1C).

Field experiment

Auditory cues decreased *Spodoptera* herbivory and increased plant biomass (Figure 2). Plants in the control treatment experienced 17% more herbivory (measured as
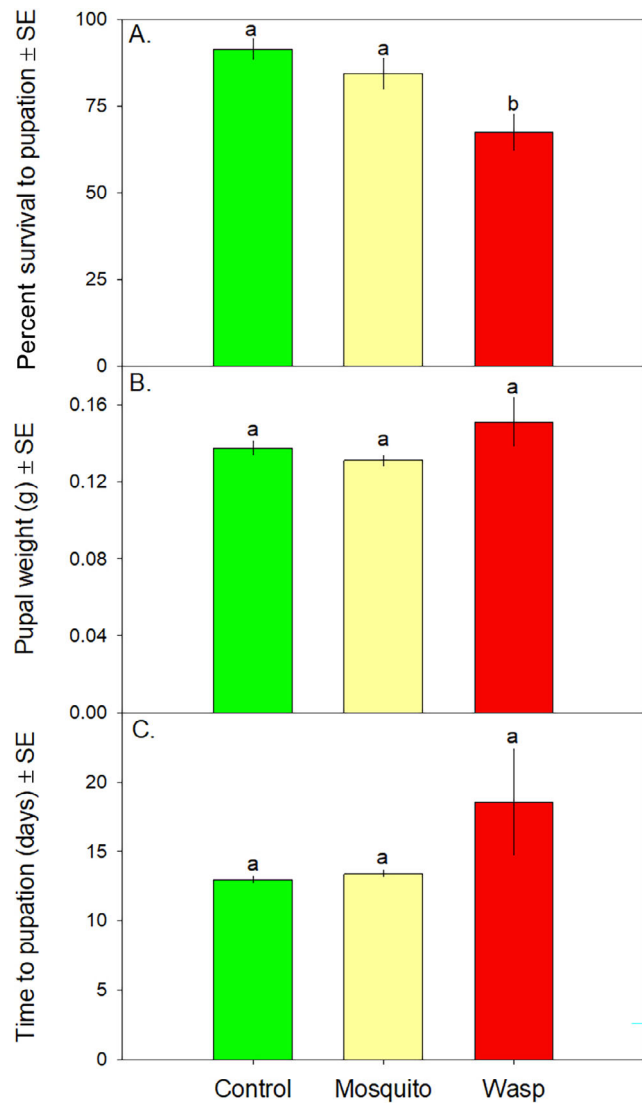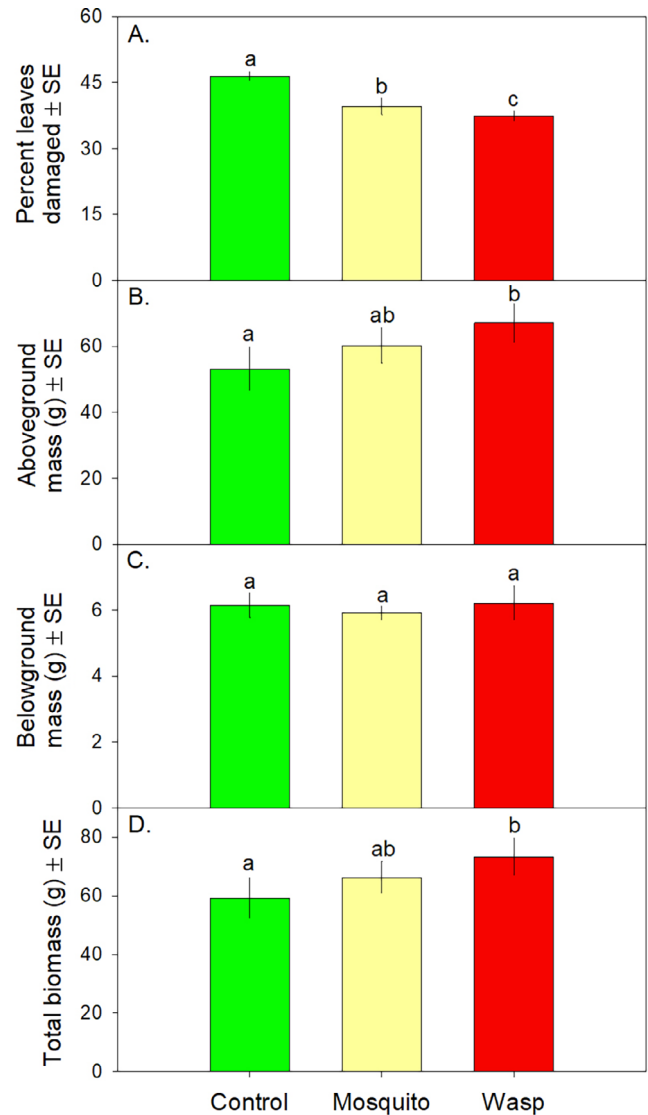
FIGURE 1 Laboratory experiment data on *Spodoptera exigua* (A) survival to pupation, (B) weight at pupation, and (C) days to pupation. Different lowercase letters denote treatment-level differences at $p = 0.05$ (Tukey's honestly significant difference test).

FIGURE 2 Field experiment data on (A) percentage of tomato plant leaves damaged by *S. exigua*, (B) aboveground plant biomass, (C) belowground plant biomass, and (D) total plant biomass. Different lowercase letters denote treatment-level differences at $p = 0.05$ (Tukey's honestly significant difference test).

the percentage of leaves with *S. exigua* damage) than plants in the mosquito treatment and 24% more than plants in the wasp treatment (parameter estimate 5.7, SE 0.58, $\chi^2 = 33.5$, $p < 0.001$; Figure 2A). The difference in herbivory was also reflected in aboveground biomass measurements (parameter estimate −8.0, SE 2.80, $\chi^2 = 8.87$, $p = 0.012$; Figure 2B). Means separation tests revealed that plants in the control treatment were significantly (21%) lighter than wasp plants but did not differ from plants in the mosquito treatment (Tukey's HSD, $p = 0.05$).

Although there were no treatment-level differences in belowground biomass (parameter estimate 0.06, SE 0.21, $\chi^2 = 1.60$, $p = 0.45$; Figure 2C), the differences in aboveground biomass were reflected in total plant biomass (parameter estimate −8.0, SE 2.88, $\chi^2 = 8.62$, $p = 0.014$;

Figure 2D). Plants in the control treatment were significantly (19%) lighter than plants in the wasp treatment, but did not differ from plants in the mosquito treatment (Tukey's HSD, $p = 0.05$). The treatments did not affect fruit production (parameter estimate −0.08, SE 0.71, $\chi^2 = 0.05$, $p = 0.98$).

DISCUSSION

Caterpillars exposed to auditory predator cues (wasp buzzing) had a lower survival in the laboratory and reduced herbivory in the field. These impacts were not

entirely a function of sound per se; responses to nonpredator cues (mosquito buzzing) were generally similar to the no-sound control treatment. The significant difference in effect between the nonpredator and predator cue treatments suggested that whereas caterpillars displayed some reaction to general sound in the field (perhaps amplified by the stress of an outdoor field setting), they recognized and responded more strongly to the sound of a predator. Social wasps such as those used in our work are voracious caterpillar predators that elicit antipredator responses in both the laboratory (Baranowski & Preisser, 2018; Tautz, 1977; Tautz & Markl, 1978) and the field (Stamp, 1997; Stamp & Bowers, 1993). Although previous research has suggested that auditory cues from wasps and related (but harmless) species such as honeybees can reduce herbivory (Tautz & Rostás, 2008), these prey responses could also have been driven by chemical and/or visual predator stimuli. Our work removed these conflating factors and showed that auditory predator cues can affect invertebrate herbivores sufficiently to reduce plant damage and increase plant biomass in the field.

Given the three-fold increase in mortality in the wasp treatment relative to the control (Figure 1A), we were surprised by the lack of any effect on time to/size at pupation in the laboratory experiment (Figure 1B,C). While we expected that predator cues stressful enough to kill some caterpillars would affect overall growth and development, the surviving caterpillars in the wasp treatment appeared unaffected by the stressor. Such sublethal predator effects, that is, RITRs and NCEs, have been widely reported in other systems (Draper & Weissburg, 2019; Sheriff & Thaler, 2014; Weissburg et al., 2014; Widén et al., 2022). Although the apparent lack of impact was unexpected, similar results have been reported in work on several other larval invertebrates. Exposing larval dragonflies to predator cues sharply increased mortality, for instance, without affecting either larval or adult body size of the surviving individuals (McCauley et al., 2011). They hypothesized that the benefits of decreased crowding and resource competition among surviving individuals may have counteracted any costs. Prior work on auditory predator cues in our laboratory also found risk effects on survival, but not on growth or development, in two other lepidopteran species (Baranowski & Preisser, 2018). The former experiment found that *Actias luna* caterpillars dying in the predator treatment gained no weight between the start of the experiment and their death, suggesting that risk-induced reductions in feeding increased larval mortality (as in Schmitz et al., 1997). Our results are also consistent with intraspecific variation in risk tolerance: "shy" individuals (sensu Sih et al., 2012) may perceive predator cues as threatening and cease feeding while "bold" individuals ignore the same stimulus. If so, the surviving caterpillars would fall into the "bold" group and thus suffer no ill effects on growth and development. The costs of predator stress early in development could also manifest during later life stages. Studying the effects of auditory risk across the life cycle of multiple generations would be a fascinating topic for follow-up research (Niitepõld & Boggs, 2022).

Our results add to a growing body of evidence that auditory predator cues can play an important role in terrestrial systems. Prey responses to predator vocalizations have been documented in a wide array of vertebrate species (Hettena et al., 2014) and can alter the population demography of free-living songbirds (Allen et al., 2022). These effects can be strong enough to benefit prey resources: in agricultural systems, predator playbacks reduce crop damage by both birds (Enos et al., 2021) and wild ungulates (Widén et al., 2022). A striking aspect of this work was how little research had been conducted using nonvertebrate species: a review of prey responses to predator sounds found that 181/183 experiments used vertebrate prey (Hettena et al., 2014). Invertebrate responses to predator vibrational cues have been found in a number of systems, but those that have disentangled this modality from other predation risk cues have done so with water- or substrate-borne vibrations (Castellanos & Barbosa, 2006; Gish, 2021; Roberts, 2017). With the notable exception of bat–insect interactions, insect responses to auditory predator cues have received minimal attention (Yack et al., 2020). The fact that "ears" evolved multiple times in lepidopteran insects alone, however, and did so prior to the appearance of echolocating bats (Kawahara et al., 2019), trumpets the importance of sound to terrestrial invertebrates and argues that this modality may play a more general role in mediating predator–prey interactions (e.g., Barton et al., 2018).

While our results suggest that auditory predator cues can alter herbivore survival and plant damage, there are several caveats that need to be considered. First, the disturbance treatment in our field experiment was calibrated via pilot work assessing the number and duration of bee and wasp visits to a flowering tomato plant. The results, while enabling us to estimate hymenopteran visit frequency and duration, may not precisely correlate with what caterpillars hear; future work might explore the soundscape produced by such visits. Second, we used commercially reared *Spodoptera* larvae in our work. Recent work in our laboratory comparing responses to auditory predator cues in wild-caught versus commercially reared populations of *Lymantria dispar* found that "wild" *Lymantria* caterpillars responded, while "domesticated" *Lymantria* lines did not. While both ourselves and previous researchers (Tautz & Rostás, 2008) found that "domesticated" *S. exigua* still responded to auditory predator cues, the effect of this stimulus on "wild" *Spodoptera*

might be substantially greater. Finally, the abundance of social wasps generally increases throughout the summer before peaking in the fall (Guedot et al., 2018; Southon et al., 2019); future work might compare the antipredator responses of spring-feeding caterpillars with those of summer-/fall-feeding species.

Because insects are the dominant herbivores in many ecosystems (Laws et al., 2018), our work has general implications for terrestrial predator–prey interactions and may be particularly applicable to the control of agricultural insect pests. RITRs and NCEs play an important role in biological control efforts (Culshaw-Maurer et al., 2020), and a review of their impacts on insect herbivores in agricultural systems listed multiple experiments using chemical and/or visual predator cues (Hermann & Landis, 2017). The fact that the latter paper did not list auditory cues as even a potential modality for prey risk assessment highlights a gap in our understanding and emphasizes the need for additional work to establish the generality of our findings.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Preisser, 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.19967528.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.