Environmental Entomology, 53(4), 2024, 587–593
https://doi.org/10.1093/ee/nvae040
Advance Access Publication Date: 15 May 2024
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Domestication reduces caterpillar response to auditory predator cues

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Subject Editor: Jason Schmidt

Received on 17 September 2023; revised on 22 December 2023; accepted on 29 April 2024

Domestication can lead to significant changes in the growth and behavior of organisms. While the threat of predation is a strong selective force in the wild, the relaxation or removal of this threat in captive-rearing environments selects for reduced sensitivity to biotic stressors. Previous work has documented such changes in other taxa, but no work has been done on domestication-related losses of predation risk sensitivity in insects. We exposed both wild and domesticated (>50 generations in captivity) *Lymantria dispar dispar* (Lepidoptera: Erebidae) larvae to recordings of predators (wasp buzzing), nonpredators (mosquito buzzing), or no sound to compare the effects of predation risk on the two stocks. Wasp buzzing, but not mosquito buzzing, decreased survival of wild caterpillars relative to the control; domesticated caterpillars showed no such response. Domesticated *L. dispar* larvae appear to have reduced sensitivity to predation risk cues, suggesting that captive-reared insects may not always be analogs to their wild counterparts for risk-related behavioral studies.

Key words: Lymantria dispar, domestication, predation risk, auditory cue, nonconsumptive effect

Introduction

Domestication, the adaptation of a population to artificial rearing conditions, occurs when the conditions and selective pressures of artificial environments differ from those in natural habitats (Hoffmann and Ross 2018). This allows for factors such as food availability and environmental conditions to be kept at optimal levels to maximize population growth or other valued traits. Such changes may also, however, alter resistance to starvation, temperature, desiccation, or other abiotic constraints and have been linked to shifts in environmental stress tolerance in captive-reared populations of the psyllid *Aphalara itadori* (Jones et al. 2021). Artificial and inadvertent selection are key drivers of these domestication-related phenotypic changes, but they can also result from inbreeding and genetic drift (Bosse et al. 2019, Perez et al. 2021). The short generation times and high fecundity of many insect species mean that these changes occur relatively quickly, making them useful for research exploring how domestication affects behavior and physiology (Liedo et al. 2007).

The changes in abiotic stress tolerance seen in captive-reared populations are often accompanied by decreased sensitivity to environmental cues (Price 1999). In laboratory settings, artificial selection for docility, crowding tolerance, and easy handling can give animals ease in conditions that free-living organisms would find intolerable (Blanchard et al. 1986, Stanley and Kulathinal 2016). Such altered response thresholds are particularly apparent in the response of captive-reared versus free-living populations to predation risk (Alvarez and Nicieza 2003, Solberg et al. 2020). In free-living organisms, the high fitness cost of a successful predator attack selects prey capable of behavioral/physiological responses. These defensive responses can be costly: dragonfly larvae exposed to predator cues experience increased mortality (McCauley et al. 2011). In contrast, the anthropogenic protection afforded domesticated organisms means that they are at little or no risk from predators and other natural enemies. As a result, energy spent on antipredator behaviors in such environments is wasted (Swaney et al. 2015). A predator-free environment thus selects individuals that allocate energy to growth and reproduction at the expense of antipredator behavior (Storsberg et al. 2018). Although domestication is generally thought to increase predator susceptibility (Solberg et al. 2020) and multiple studies have explored the effects of domestication on insects (Hoffmann and Ross 2018), we are unaware of any research exploring how it affects their responses to predation risk.

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The spongy moth (*Lymantria dispar dispar*; "*Lymantria*"; Lepidoptera: Erebidae), a generalist herbivore, is an ideal model system for exploring how domestication affects insect responses to predator cues. It was introduced into the United States in the 1890s and quickly became a devastating forest pest (Liebhold et al. 2021). Because of its substantial economic impacts, a laboratory colony collected in the invaded range has been maintained in captivity for research since 1967 (Keena and O'Dell 1994). *Lymantria* remains easily found in the forests of the northeastern United States, so both lab-reared and wild-collected *Lymantria* are readily available. Research comparing these two strains found that lab-reared individuals differed in their pheromone production and sexual behavior (Richerson and Cameron 1974), developed more quickly, underwent a shorter diapause, and had higher fecundity than did wild-collected individuals (Grayson et al. 2015). Another comparison of these populations found lab-reared *Lymantria* moths had wider variation in their response to auditory cues than wild-collected adults, a result the authors suggested could reflect reduced predation pressure (Cardone and Fullard 1988). We classify the lab-reared *Lymantria* population as domesticated according to the 5-step "domestication level" classification system (Lecocq 2019) that rates captive populations from 1 (wild population relocated to the human-controlled environment) to 5 (selective breeding and\or bioengineering for specific traits). The lab-reared *Lymantria* population meets the criteria for level 4 (full human control of life cycle in artificial environments without external gene flow) of this classification system.

We report the results of research measuring the growth, development rate, and survival of wild-type and domesticated *Lymantria* larvae exposed to auditory predator cues (prerecorded wasp buzzing), auditory nonpredator cues (prerecorded mosquito buzzing), or a no-sound control treatment. Predator and nonpredator cues were played at the same volume and periodicity to control for the effect of sound per se. Larvae of over 30 different lepidopteran species respond to sound behaviors that range from freezing to aggression (reviewed in Taylor and Yack 2019). Exposing caterpillars to auditory predator cues is an effective way to elicit antipredator behavior (Breviglieri and Romero 2019, Taylor and Yack 2019, Lee et al. 2021, 2023) and allows us to compare the levels of sensitivity to predation risk between the two stocks. *Lymantria* larvae are attacked by predatory wasps and well over 100 species of hymenopteran parasitoids (Furuta 1983, Boukouvala et al. 2022), providing a survival advantage to individuals capable of detecting and responding to buzzing. Because lab-reared *Lymantria* are less active than their wild counterparts (Richerson and Cameron 1974), we hypothesized that they would also be less responsive to predation risk.

Materials and Methods

Acquisition and Rearing

In July 2020, wild *L. dispar* larvae were collected from various host plants at the University of Rhode Island East Farm Research Facility (Kingston, RI, USA; 40.742, –73.989) and reared in a laboratory under ambient light and controlled temperatures (20–22 °C). This was a sparse *L. dispar* population (<1 egg mass/tree, ~20 egg masses/ha) that would be considered low density (Myers et al. 1998). It had its last outbreak in 2017 and has been at low densities since 2019. To guard against the possible spread of field-acquired pathogens, larvae were housed separately in 118 ml polypropylene cups with airtight lids and fed sweetgum (*Liquidambar styraciflua*) leaves that had been sprayed with a 2% bleach (0.6% sodium hypochlorite) solution and allowed to air dry. Pupae were sexed, and individual pairs of male-female pupae were transferred into 473 ml paper cups. Adults mated within these cups, and females oviposited along the cup walls. Individual egg masses were transferred to a separate 473 ml clear polypropylene cup with airtight lids. A 3 cm × 3 cm moistened paper towel square was placed in the bottom of each cup to prevent desiccation. Egg masses were maintained at controlled temperatures (20–22 °C) until late October when they were transferred to a 7 °C cooler. In October 2020, we obtained egg masses (USDA permit # P526P-18-01749) from a long-term lab colony maintained for research purposes by the Otis USDA APHIS lab (Buzzard Bay, MA, USA) for 80 generations (Nadel et al. 2020); these egg masses were placed in the same 7 °C cooler at the same date. In April 2021, all egg masses were removed from the cooler and placed in ambient temperatures to emerge. All emerging caterpillars were fed fresh crabapple foliage (*Malus* sp.) and kept in 950 ml clear plastic cups (approx. 200 per cup) until the start of the experiment.

Experimental Design

The experiment was conducted using 240 third-instar caterpillars that had molted the previous day. The newly molted caterpillars from the two lineages (120 wild-types and 120 domesticated) were randomly assigned to 1 of 3 auditory risk treatments: the buzzing of a predatory insect (*Mischocyttarus* sp. Hymenoptera: Vespidae; caterpillar-hunting paper wasp), buzzing of a harmless insect (*Aedes* sp.; Diptera: Culicidae; mosquito), and no-cue control. Similarly sized vespid wasps are voracious predators of *Lymantria* larvae (e.g., Furuta 1983), and we have locally observed *Polistes* sp. vespids feeding on them in late spring (Preisser, *unpublished data*). Our experiment thus crossed caterpillar lineage (wild-type, domesticated) with predation risk (wasp buzzing, mosquito buzzing, control) for a total of 6 treatments, with 40 caterpillars per treatment. Styrofoam coolers were used to reduce the risk of sound transmission between treatments. We used a BAFX 3370 dB m (BAFX Products LLC, Muskego, WI, USA) decibel meter to measure levels of transmission: sound transmission from one box to the next was measured at <2 dB, while sound treatments within the boxes were measured to provide an 18–20 dB increase over ambient levels. Lighting within the boxes was provided by LED light strips that were turned on from 8 AM to 8 PM. Sound treatments were only played during the 12-h lighted period.

The 40 caterpillars in each treatment were randomly split into eight 5-caterpillar groups (= replicate); each group was held individually in a 473 ml polypropylene cup. We weighed each 5-caterpillar set to determine the initial larval weight per cup; this data was used as a covariate in our models (see below). Four cups containing 5 caterpillars each were then placed in each of 12 Styrofoam coolers. In each cooler, 2 cups contained domesticated larvae and 2 contained wild-type larvae (Fig. 1). Each cooler contained a speaker (NiZHi TT-028, Shenzhen Powerunion Technology Co., Guangdong, China) playing the sound treatment: caterpillars in the harmless sound treatment were exposed to a recording of harmless mosquito (*Aedes* sp.) buzzing (613.6 ± 141.0 [SD] Hz), while the predator treatment groups were exposed to a recording of predatory wasp (*Mischocyttarus* sp.) buzzing (187.5 ± 1.5 [SD] Hz). The no-sound control group speakers played a loop of silence to control for the possible effects of the speaker (visual effects, heat, etc.). Both insect sound files (mosquito and wasp) were generously provided by Drs. C. Breviglieri and G. Romero (University of Campinas, Sao Paulo, Brazil); detailed information on bandwidth, harmonics, and microphone specifications is provided elsewhere (Breviglieri and Romero

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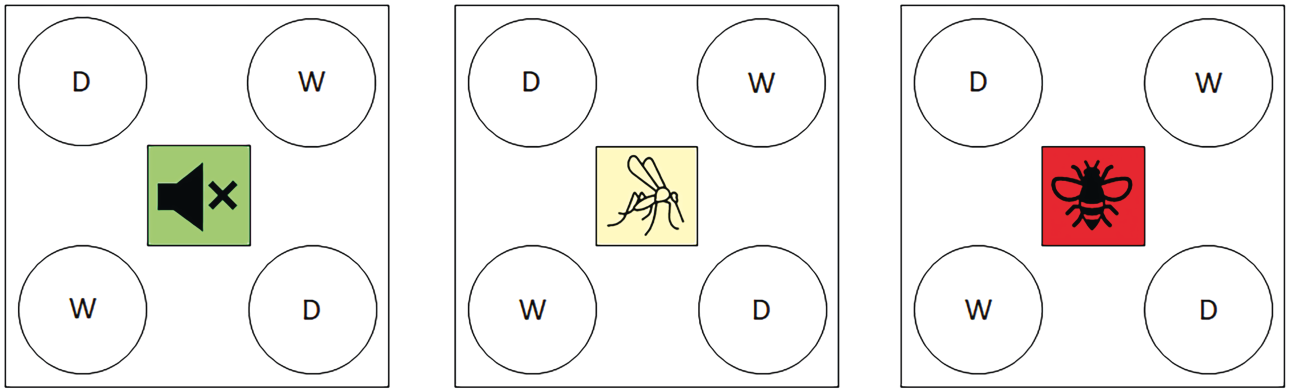

Fig. 1. Arrangement of replicates within coolers. Coolers were assigned to either a no-sound treatment (left-hand box), mosquito buzzing (middle box), or wasp buzzing (right-hand box). "W": replicates (cups) containing wild-type *L. dispar* larvae; "D": replicates containing domesticated *L. dispar* larvae. Each replicate cup contained 5 caterpillars, and there were a total of 8 replicates per risk*stock combination. Speakers within each cooler produced the sound treatments.

2019). These files have been used in previous research assessing behavioral responses of caterpillars to auditory predation, and the wasp buzzing has been shown to elicit antipredator behavior in *Hylesia nigricans*, *Danaus plexippus*, and *Spodoptera exigua* (Breviglieri and Romero 2019, Lee et al. 2021, 2023). Wasp and mosquito sound files were set to run for 2-second intervals, repeating every 6 s, from 8 AM to 8 PM. The rationale behind this exposure frequency is detailed in the discussion; briefly, this protocol is consistent with previous work and has successfully elicited antipredator responses in caterpillars (Lee et al. 2021). Caterpillars were fed fresh crabapple (*Malus* sp.) foliage ad libitum, with daily checks to replace any wilted foliage with new material. Caterpillars were checked daily for mortality and pupation. Survival to pupation as well as the time to pupation and weight of each pupa, was recorded; the latter information was used to calculate the mean time to pupation and mean pupal weight per cup. All pupae were also sexed; because male and female larvae are externally identical, we were unable to determine the gender of deceased larvae.

Statistical Analysis

The unit of replication for this experiment was mean response per 5-larva cup. Prepupal mortality was analyzed using the R stats package for GLM (normal distribution, identity link function), the main effects treatment, stock, and treatment*stock, and initial larval weight as a covariate. Because we were interested in whether larvae survived to pupation (rather than when they died), we analyzed mean survival per cup rather than changes in individual survival over time. Time to and weight at pupation were analyzed using the same main effects and both initial larval weight and % female at pupation (female larvae pupate later and at a larger size than male larvae) as covariates. Time to death was analyzed using individual larvae as the replicate and the main effects of treatment, stock, and treatment*stock. Response variables were normally distributed. Initial models included coolers as a blocking variable, but this was not found to be a significant covariate and was removed from subsequent models. Because low-density wild *Lymantria* populations can have higher F:M pupal sex ratios (Myers et al. 1998, Campbell 2012) than the 50:50 occurring in the lab population (Grayson et al. 2015), we also tested whether the pupal sex ratio varied as a function of treatment, stock, and the treatment*stock interaction.

All analyses were conducted using R 4.2 0 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Prepupal Mortality

Both stock (χ^2_1 $df = 28.6$, $P < 0.001$) and treatment (χ^2_2 $df = 13.2$, $P = 0.001$) significantly affected prepupal mortality. Wild-type larvae suffered higher mortality than domesticated larvae (37% ± 4.2% [SE] vs. 13%±2.8%, respectively). Mortality in the wasp treatment (36% ± 6.3%) was higher than mortality in the control treatment (15% ± 4.3%; Tukey's HSD with $\alpha = 0.05$); mortality in the mosquito treatment (25% ± 4.0%) differed from neither the wasp nor control treatments. The significant effect of treatment was driven by a strong response of wild-type larvae to a wasp buzzing; prepupal mortality in domesticated larvae was not affected by treatment (treatment*stock interaction: χ^2_2 $df = 6.09$, $P = 0.048$). There was also a significant effect of initial larval weight (χ^2_1 $df = 4.03$, $P = 0.045$). Wild-type larvae died more quickly than domesticated larvae (13 ± 1.6 days [$n = 43$] vs. 21 ± 3.4 days [$n = 16$]; χ^2_1 $df = 4.43$, $P = 0.035$), but time to death was not affected by either treatment or the treatment*stock interaction (both $P > 0.4$) (Fig. 2A).

Time to Pupation

Mean time to pupation per cup varied significantly by larval stock (χ^2_1 $df = 8.38$, $P = 0.0038$), with domesticated larvae pupating 13% faster than wild larvae (30 ± 0.8 days vs. 34 ± 0.9 days, respectively). Neither treatment, the treatment*stock interaction, nor the covariates affected time to pupation (all $P > 0.05$) (Fig. 2B).

Weight at Pupation

Although deceased larvae were not weighed because we could not sex them, larval stock significantly affected mean pupal weight per cup (χ^2_1 $df = 20.7$, $P < 0.0001$). Probably because of their longer time to pupation, cups of wild-type larvae had higher mean pupal weights (0.81 ± 0.04 [SE] g) than domesticated larvae (0.56 ± 0.03 g). While there was no effect of treatment or the treatment*stock interaction (both $P > 0.05$), mean pupal weight per cup was significantly affected by both initial larval weight (χ^2_1 $df = 7.15$, $P = 0.008$) and % female pupae per cup at pupation (χ^2_1 $df = 36.9$, $P < 0.001$) (Fig. 2C).

Pupal Sex Ratio

The two stocks differed in their pupal F:M sex ratio (χ^2_1 $df = 8.51$, $P = 0.004$), with the domesticated stock having a roughly even

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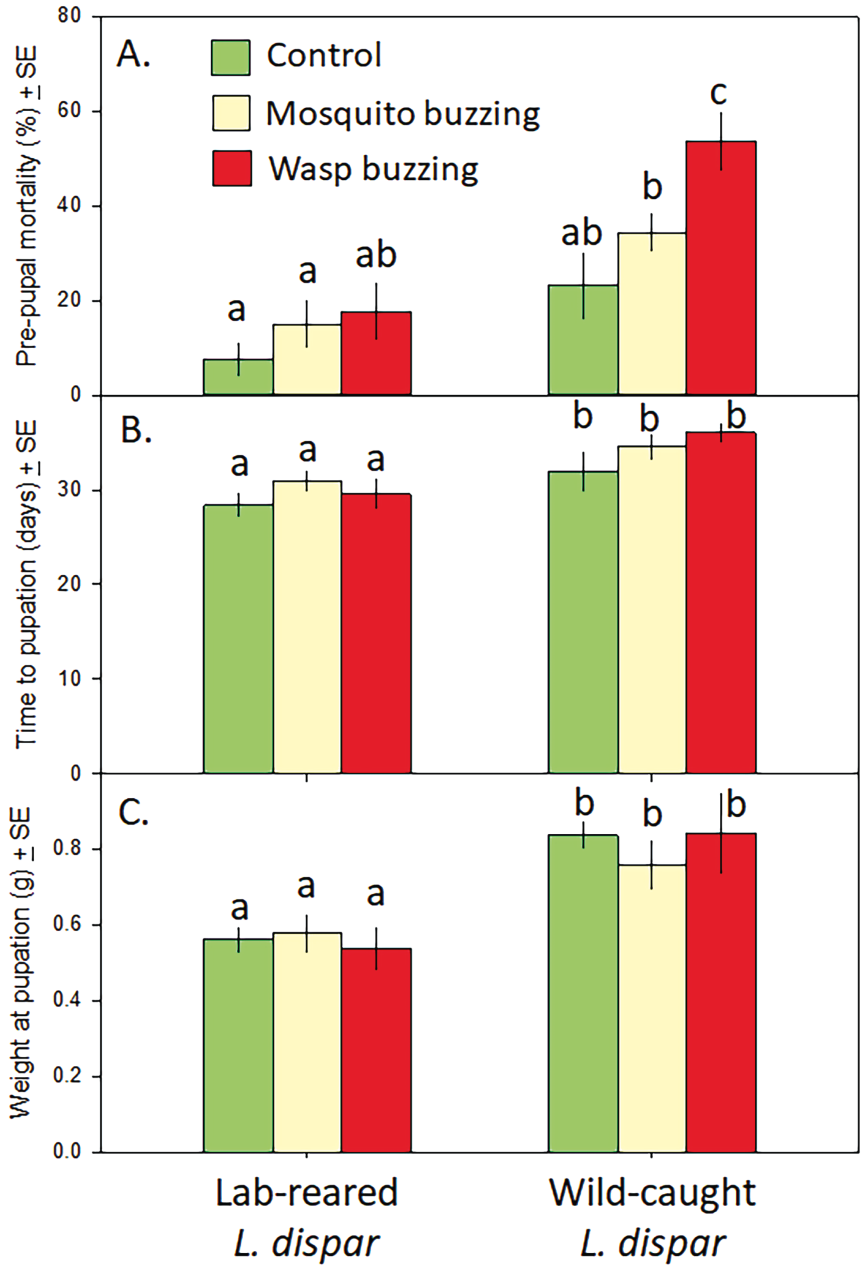

Fig. 2. Prepupal mortality: A), time to pupation B), and pupal weight C) of domesticated and wild-type *L. dispar* larvae exposed to either no-cue control, mosquito buzzing, or wasp buzzing. Bars represent means ± SE of 8 cups (replicates) per treatment; the number in each bar indicates the total number of larvae. Lowercase letters denote significant differences at $\alpha = 0.05$ (Tukey's HSD).

ratio (45.4 + 4.9 SE; $n = 24$) while the wild stock was female-biased (69.6 ± 6.8 SE; $n = 24$). The pupal sex ratio did not differ by treatment, however, and the treatment*stock interaction was not significant (both $P > 0.2$). There was also no relationship between mean prepupal mortality per cup and pupal sex ratio per cup ($F_{1,46} = 0.09$, $P = 0.77$).

Discussion

Auditory predator cues increased prepupal mortality in wild-type larvae but not their domesticated counterparts. The fact that auditory cues from a harmless insect did not evoke a similar response suggests that wild-type larvae were specifically reacting to the buzzing of a predator rather than to sound per se. The increase in prepupal mortality, perhaps due to risk-induced feeding cessation, demonstrates that chronic predator stress can be fatal to lepidopteran larvae. The domesticated caterpillars, however, showed no difference in prepupal mortality between the sound treatments. Reduced responses to predation risk are found in domesticated populations of a wide variety of species (Alvarez and Nicieza 2003, Brokordt et al. 2006, Geffroy et al. 2020, Solberg et al. 2020); our results suggest that similar changes occur in insects.

Neither wild-type nor domesticated caterpillars showed any treatment-level differences in time to pupation or pupal weight. We had anticipated that individuals would show a gradated stress response, with more affected individuals dying and less affected

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individuals exhibiting altered growth and development. Instead, it appears that the individual-level response to risk was bimodal—larvae either died or were unaffected. While unexpected, this result is consistent with previous work (McCauley et al. 2011) exploring the response of larval odonates to predator risk. In their experiments, exposure to caged predators increased prepupal mortality but affected neither the larval nor adult body size of the surviving individuals. They suggested that this may reflect the negative effects of risk on the surviving larvae being compensated for by reduced competition and lower foraging costs (McCauley et al. 2011); a similar dynamic may occur in our system. The lack of an effect on surviving larvae may also be explained by the populations differing in their proportion of risk-averse versus risk-tolerant individuals, e.g., the shy-bold behavioral syndrome (Sih et al. 2012). While predation on wild populations favors individuals that respond strongly to predator cues, lab rearing reduces or eliminates such selection (see below). This is consistent with prior work on our two *Lymantria* stocks that found greater variation in responses to auditory cues in the domesticated population (Cardone and Fullard 1988). If our treatments affected risk-averse individuals but not their risk-tolerant counterparts, it would explain both the higher mortality in wild versus domesticated populations and the lack of a growth/development response in the surviving individuals. This interpretation is supported by our finding that larval mortality occurred earlier in the wild population than in the domesticated one. As the behavioral syndrome hypothesis encompasses a wide range of behaviors besides just predator sensitivity (foraging behavior, movement speed, risk-taking), further comparisons on other factors would be useful in identifying whether the shy-bold behavioral syndrome paradigm is appropriate.

Domesticated caterpillars are pupated more quickly and at a lower weight than wild-type caterpillars. This decrease in development time is consistent with prior work on our lab-reared *Lymantria* population (Grayson et al. 2015) that found domesticated larvae pupated more quickly and also at a higher weight than wild-type larvae when reared on red oak. This difference is likely a function of the fact that the wild population had a higher F:M pupal sex ratio than the domesticated one. The 70:30 F:M ratio in our wild population is essentially identical to that found in other low-density wild *Lymantria* populations (Myers et al. 1998, Campbell 2012); conversely, the 50:50 ratio in the lab population is also typical for this stock (Grayson et al. 2015). Because female pupae weigh more than males, the greater number of females in the wild population likely explains the higher mean pupal weight in that stock. Alternately, the fact that wild-type larvae pupated at a higher weight in our work may reflect our use of a different wild population, differences in diet, or other rearing conditions. Although it would have been ideal for rearing the larvae through to adulthood and assessing mature individuals, our permit for this work required that pupae from the domesticated population be destroyed prior to emergence.

Our experiment was originally inspired by behavioral differences between the wild and domesticated stocks (also noted in Richerson and Cameron 1974), and the stark difference in sensitivity to predation risk suggests a domestication-related loss of antipredator behavior. Domestication-related changes in oviposition or activity that render individuals "…far tamer and more manageable" have been seen in a number of insect species, including fruit flies, silkworms, and psyllids (Stanley and Kulathinal 2016, Komoto 2017, Jones et al. 2021); in some cases, this change can be seen after as few as two generations in captivity (de Mestral and Herbinger 2013). This loss of sensitivity could be due to several factors. Mass-rearing environments are highly stressful to wild insects, selecting for high levels of stress tolerance (Hoffmann and Ross 2018). As predators pose no risk in captivity, any energy put into predator detection/antipredator behavior is wasted, potentially giving a fitness advantage to those who invest more energy into growth and reproduction (Swaney et al. 2015). The increased larval weight and decreased development time in the domesticated *Lymantria* (Grayson et al. 2015), coupled with greater variability in their responses to auditory cues (Cardone and Fullard 1988), suggests that a similar dynamic may be at play in this system. Specifically, the precise mechanism of mortality needs to be established. While caterpillars exposed to wasp buzzing often froze, we did not take specific data on the length of time spent motionless and whether increased freezing rates correlated with lower weight gain (and, in some cases, eventual death) of specific larvae.

In a larger context, our findings caution against extrapolating the results of experiments using lab-reared insects onto wild populations. While lab-reared insects may be genetically indistinguishable from their free-living kin, domestication-related changes in behavior and physiology may make them unreliable analogs to their wild counterparts. Specifically, the responses of domesticated insects to predator cues may tell us little about how these stressors affect free-living populations (a phenomenon also noted in rats; Blanchard et al. 1994). This has implications for studies on insect behavior and reactions to predation risk, where captive-reared insects are often used for convenience and availability (Hermann and Thaler 2014, Kempraj et al. 2020, Lund et al. 2020, Piovezan-Borges et al. 2020, Humphreys et al. 2021). In our case, the impact of auditory predator cues on wild-type caterpillars suggests the potential for using sound to reduce herbivory as part of an integrated pest management plan (Lee et al. 2023).

While our results highlight differences in risk sensitivity between domesticated and wild insects, there are a few caveats that need to be considered. We exposed caterpillars to auditory cues constantly over an extended period, with cues playing for two seconds every 8 s for 12 h a day. This exposure regime has been shown to successfully elicit responses in caterpillars (Lee et al. 2021) and was chosen to maximize the likelihood of observing an effect. Such chronic exposure is almost certainly higher than what occurs in the wild, and future studies should explore whether lower exposure levels induce similar responses. Because differences in activity levels between wild *Lymantria* and our domesticated population have already been noted (Richerson and Cameron 1974), our study focused specifically on the effect of predator cues on mortality, growth, and development time; additional studies should explore risk-induced changes in behavior between wild-type and domesticated caterpillars. Another unavoidable limitation of our research is that there is currently only a single domesticated *Lymantria* population available for our work (although there are two stock colonies, the second is ~20 years younger and was established using individuals from "our" population; Keena and O'Dell 1994). Because domestication results from selective breeding (a.k.a. inbreeding; Bosse et al. 2019), it is also possible that inbreeding depression accompanying the domestication process could underly our results; it would be fascinating to carry out similar research on insects with multiple independent domestication events. Other potential future studies involve field trials in more natural environments and investigations into the reactions of both caterpillar stocks to live predators. Although vespid wasps can and do prey on *Lymantria*, they exert less of a toll in the late spring/early summer than do parasitoids (Furuta 1983, Boukouvala et al. 2022); it may be that the frequencies of our wasp recording were close enough to those of parasitoids to induce a response. Caveats aside, however, we believe this study to be the first to demonstrate a domestication-related loss of antipredator behavior in insects.

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Acknowledgments

The comments of two anonymous reviewers greatly improved this manuscript. We thank Drs. Crasso Paulo B. Breviglieri and Gustavo Q. Romero for the use of their audio files. We also thank the USDA APHIS Forest Pest Methods Lab for providing the domesticated *L. dispar* population used in this experiment. Doctors Steven Alm, Lisa Tewksbury, and Jason Kolbe provided helpful feedback on the manuscript.

Funding

This research was supported by the United States Department of Agriculture under McIntire-Stennis project RI0020-MS986 to E.P.

Author Contributions

Zachary Lee (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Project administration [equal], Writing—original draft [equal], Writing—review & editing [equal]), Caroline Cohen (Investigation [equal], Methodology [equal]), Tyler Pelletier (Investigation [equal], Methodology [equal]), Evan Preisser (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Resources [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal]), and Alex Baranowski (Conceptualization [supporting], Investigation [equal], Methodology [equal], Project administration [equal], Writing—original draft [equal])

Data Availability

All data are archived on figshare (https://doi.org/10.6084/m9.figshare.25683921.v1). This will be the permanent repository.

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