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# Critical thermal limits of the seasonal migrant, *Euxoa auxiliaris* (Lepidoptera: Noctuidae)

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The larval stage of the army cutworm, *Euxoa auxiliaris* (Grote), is an agricultural pest in the Great Plains region of North America. Adult migration to alpine aggregation sites to escape extreme summer temperatures and depleted food resources provides a critical food resource for the grizzly bear, *Ursus arctos horribilis* (Linnaeus, Carnivora: Ursidae), in the Rocky Mountains. However, little is understood about the ecological consequences of the thermal tolerance of adult *E. auxiliaris*. Therefore, we investigated thermal tolerance of lab-reared and wild-caught individuals by assessing their critical thermal limits ($CTL_{max}$ and $CTL_{min}$). Using a ramping tolerance assay, we began at 25 °C and adjusted the temperature at a rate of 0.3 °C/min until individuals lost control of their righting response. Adult moths had a $CTL_{max}$ (lab-reared: 44.13 °C, wild-caught moths: 43.28 °C) typical for a temperate lepidopteran species. However, their $CTL_{min}$ (lab-reared: −2.24 °C, wild-caught: −1.9 °C) reflects an extraordinary ability to remain active and feed when ambient temperatures are low. These findings provide insights into the thermal ecology of *E. auxiliaris* which are essential for predicting the range distribution of the species, and, consequently, the continued availability of this key food source for Rocky Mountain grizzly bears. As climate change continues to affect ambient temperatures, these results underscore the importance of studying thermal tolerance to anticipate ecological shifts and ensure the conservation of both *E. auxiliaris* and the grizzly bears that depend on them.

*Keywords:* army cutworm, Rocky Mountains, Great Plains, temperature tolerance, migration

## Introduction

As ectotherms, insects are constrained by physiological limitations imposed by abiotic factors such as temperature, precipitation, and relative humidity (Stange and Ayres 2010). Seasonally cyclical environmental conditions play an essential role in shaping life history traits and ecological niches of insects. Climatic variability imposes considerable fitness costs on insect populations, affecting survival, reproductive success, distribution patterns, population density, and the timing of key life events such as migrations (Sgrò et al. 2016, Kellermann and van Heerwaarden 2019). Consequently, individuals experience physiological variations in response to meteorological or climatic conditions (Bowler and Terblanche 2008). For example, increasing temperatures in the mid- to high-latitudes of the Northern Hemisphere can alter the abundance and distribution of various lepidopteran species, in contrast to tropical populations of the same species (Parmesan et al. 1999).

Although the effects of climate change on the environment are often modeled using large-scale climate patterns—such as global or regional trends—these approaches tend to underrepresent the impacts of climatic variability and rapid shifts on ecosystems (Thornton et al. 2014, Neuvonen and Virtanen 2015). To better assess the risk of climate variability and climate change on insect populations, estimates of thermal limits are often used (Chown et al. 2009). These limits are measured through bioassays designed to estimate critical thermal limits (CTL), which define the upper ($CTL_{max}$) and lower ($CTL_{min}$) temperature thresholds within which an individual can function. These CTLs are typically determined through a ramping tolerance bioassay, in which the temperature is gradually increased or decreased until the insect fails to exhibit a critical response or behavior, typically characterized by the loss of righting response or cessation of activity (Chown et al. 2009). Studies of insect CTLs allow for bottom-up predictions of how climate-driven

changes may affect species' distribution and abundance, highlighting the importance of physiological variation in the adaptive responses of species to changing environmental conditions (Chown et al. 2010).

The army cutworm moth, *Euxoa auxiliaris* (Grote), is a migratory noctuid with a U.S. range that spans the Great Plains to the Rocky Mountains (Burton et al. 1980, White et al. 1998). Upon emergence as adults, *E. auxiliaris* migrates west following the spring flower bloom to the Rocky Mountains, spending the summer months in alpine environments feeding nocturnally on nectar and aggregating diurnally in interstitial talus (Pruess 1967, Burton et al. 1980, French et al. 1994). These annual moth aggregations are a critical summer food source for the grizzly bear, *Ursus arctos horribilis* (L.), particularly in the Greater Yellowstone Ecosystem (GYE) due to their high caloric concentration and convenient, abundant availability during hyperphagia (French et al. 1994).

*Euxoa auxiliaris* is believed to be heat averse and cool tolerant (Pepper 1932, Chapman et al. 1955, Pruess 1967). This thermal preference may be a motivating factor for the westward and higher elevational migration of the species, as individuals cannot survive the high summer temperatures of the Great Plains (Pepper 1932). In alpine areas where the moths aggregate, temperature gradients can be considerable—ranging within talus fields from approximately 40 °C at the rock surface to below freezing at the soil surface (French et al. 1994). This gradient limits the moths' ability to escape excavation, affecting the feeding activity of the bears that feed on them (Mattson et al. 1991, French et al. 1994).

Adult *E. auxiliaris* exhibit oogenesis flight syndrome (Pruess 1967). During their westward migration and subsequent summer occupancy in alpine areas, female moths lack developed ova (Kevan and Kendall 1997). On the alpine landscape, moths engage in nocturnal feeding, which increases their abdominal lipid content, supporting sexual maturation and remigration to natal ranges in the fall for oviposition (Pruess 1967, Kevan and Kendall 1997).

Given the energetic requirements associated with reproduction and migration of *E. auxiliaris*, it is important to examine how temperature affects metabolic rate, as these effects have implications for energy storage and use in insects (Arrese and Soulages 2010). This influence on metabolic processes is substantial, for example, Bawa et al. (2021) and Shah et al. (2021) found that increasing temperatures adversely affect the metabolic efficiency of another migratory noctuid, the native budworm, *Helicoverpa punctigera*. Because of the uncertainty surrounding the effect of temperature on *E. auxiliaris* and their significance to grizzly bear conservation, it is essential to understand the moth's thermal limits.

Therefore, we investigated the upper and lower temperature tolerances of lab-reared and wild *E. auxiliaris* by measuring the $CTL_{max}$ and $CTL_{min}$ of individual moths through a ramping tolerance assay. We hypothesized that due to their migratory behavior, the moths are cold tolerant and heat averse, resulting in lower-than-average $CTL_{max}$ and lower-than-average $CTL_{min}$ for a lepidopteran species.

## Methods and Materials

### Lab-Reared *Euxoa auxiliaris*

In 2022, live adult *E. auxiliaris* were collected in Bozeman, MT. Moths were captured in blacklight traps (#2851A Universal Collecting System, BioQuip Products, Inc., Rancho Dominguez, CA) and pheromone traps baited with Scentry Army Cutworm Lures 12/CS (Scentry Biologicals Inc., Billings, MT) during the fall (late September to mid-October). Moths were transported at ambient temperatures and transferred to metal rearing cages (BioQuip Products, Inc., Rancho Dominguez, CA) for oviposition. Rearing cages contained 20 to 30 moths each and were provided with paper towels for cover. Moths were provisioned via a cotton ball soaked with a 10% sugar solution, which was replaced daily. An 85-mm diameter petri dish was placed in the bottom of each rearing cage and filled with steam-sanitized soil that had been sifted through an 8-gauge wire mesh sieve. Petri dishes were checked daily for eggs with a stereo microscope (Leica M80,Teaneck, NJ). Petri dishes with eggs were placed in vented plastic containers and stored in complete darkness at ambient temperatures of 22 to 27 °C and 50 to 60% relative humidity (RH) until hatch (Jacobson and Blakely 1959).

Second generation larvae were used for CTL assays. Larvae were reared at 22 to 27 °C and 50 to 60% RH under a 12:12 light-dark photoperiod. Larvae were fed a multiple species diet (Southland Products Inc., Lake Village, AR) supplied in 30-ml deli cups with perforated lids and replaced every 4 to 6 d based on frequency of feeding and condition of diet. Pupation occurred inside the diet cups. Pupae were left undisturbed for 3 to 4 d within the cups to minimize the risk of damaging the newly formed pupae. After 3 to 4 d, pupae were transferred from individual diet cups onto paper towel-lined, ventilated 5.7-L plastic containers. Approximately 25 to 35 pupae were placed in each container. Pupae were retained in total darkness at ambient temperatures of 22 to 27 °C and 50 to 60% RH. Paper towels were misted with deionized water every other day to provide moisture to the developing pupae. Once the pupae darkened sufficiently, they were transferred to the bottom of a rearing cage to provide a suitable environment for eclosion. Emerging adults were transferred to 0.94-L wide mouth glass jars with a metal screen lid. Each jar contained 1 to 5 moths. Jars were lined with paper towels and moths were supplied with a cotton ball soaked with 10% sugar solution and maintained under similar temperature and light conditions as larvae.

### Wild-Caught *Euxoa auxiliaris*

To determine if responses of lab-reared moths were similar to wild moths, in September 2023, live adult moths were collected in Bozeman, MT using blacklight traps and pheromone traps baited with Scentry Army Cutworm Lures 12/CS (Scentry Biologicals, Inc., Billings, MT). Moths were transported at ambient temperatures and transferred to metal rearing cages (BioQuip Products, Inc., Rancho Dominguez, CA) and stored at ambient temperatures of 22 to 27 °C and 50 to 60% RH until experimental testing. Each cage contained 20 to 30 moths, and paper towels were provided for cover. Moths were fed a 10% sugar solution provided on a soaked cotton ball, which was replaced daily. Wild-caught moths were used for experimental testing within 1 to 12 d after collection.

### Maximum Critical Thermal Limit

For all $CTL_{max}$ trials, 5 moths were individually placed in 20-ml glass vials arranged in a vial rack and submerged in heated water (Fig. 1). Acclimation took place in a 28.6 cm × 26.7 cm × 19.7 cm, 12-L clear square polycarbonate container (Rubbermaid, Atlanta, GA). The container was filled with 7 L of DI water. A submerged heating element (Joule sous vide, Breville, Compton, CA) maintained the water temperature at 25 °C during acclimation and at predetermined temperatures during testing (Fig. 1). Moths were acclimated for 10 min at 25 °C before temperature stress treatments were initiated (Keosentse et al. 2021). Following acclimation, moths were stressed at a rate increase of 0.3 °C/min (Chown et al. 2009, Bawa et al. 2021, Keosentse et al. 2021).

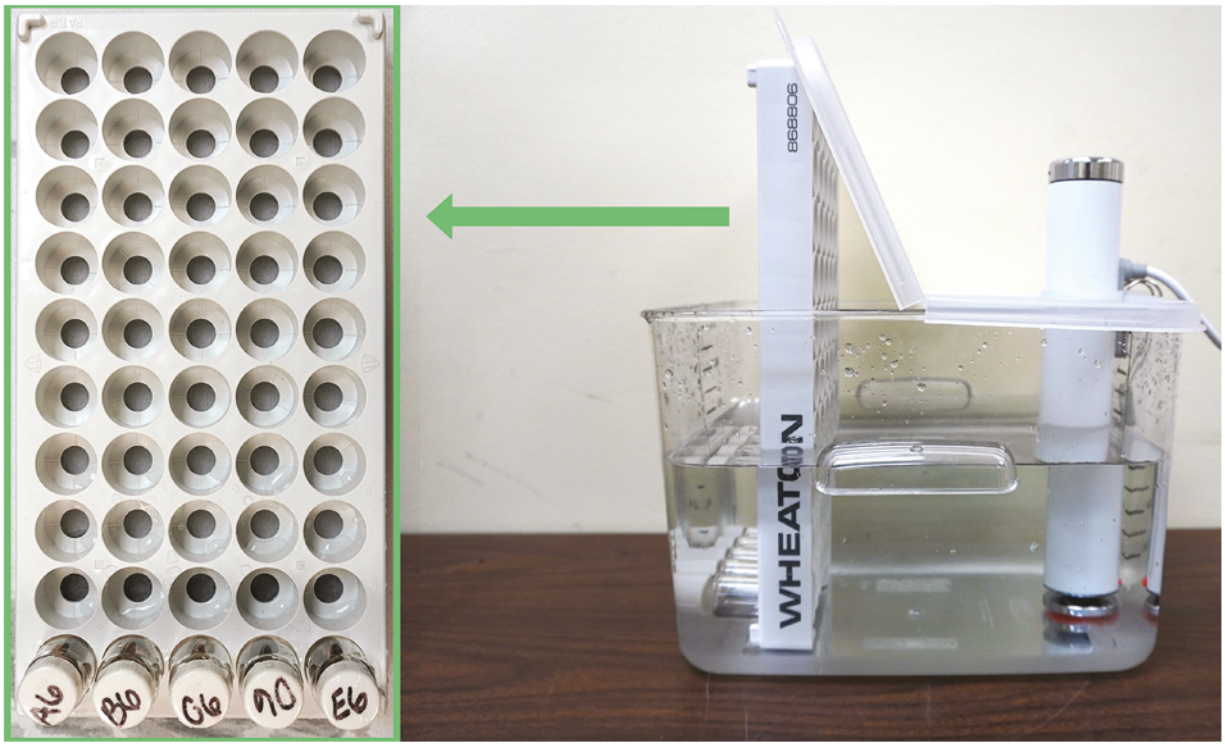


**Fig. 1.** Critical thermal maximum ($CTL_{max}$) ramping assay. Loaded vial rack used to hold submerged subsample vials (left). Sous vide and vial rack submerged in improvised water bath (right). Individual vials each containing one moth can be seen in the bottom row of the rack.

The $CTL_{max}$ was defined as the temperature at which a moth lost its righting response within a submerged vial (Toolson and Hadley 1974, Worthen and Haney 1999). Moths were removed from the water bath once all moths reached their respective individual $CTL_{max}$. A total of 8 trials were conducted using lab-reared moths, age 1 to 11 d post emergence, and a total of 9 trials were conducted using wild caught moths. The water bath was the experimental unit, and each moth in a vial was a subsample. Therefore, a sample was each trial.

## Minimum Critical Thermal Limit

For each $CTL_{min}$ trial, 5 moths were individually placed in 20-ml glass vials. The neck of each vial was fitted into a 2.5-cm hole cut into a 0.16-cm thick aluminum sheet and secured by a zip tie (Fig. 2). The aluminum sheet was submerged into a programmable water bath (PolyScience, Niles, IL) filled with polycool mix −25 °C (PolyScience, Niles, IL) (Fig. 2). Moths were acclimated for 10 min at 25 °C before temperature stress (Keosentse et al. 2021). Moths were cooled at a rate of 0.3 °C/min (Chown et al. 2009, Bawa et al. 2021). The $CTL_{min}$ was defined as the temperature at which a moth lost its righting response within a submerged vial (Toolson and Hadley 1974). Moths were removed from the water bath once all moths reached their respective individual $CTL_{min}$. A total of 8 trials were conducted using lab-reared moths, 3 to 16 d post emergence, and 9 trials were conducted on wild-caught moths. The water bath was the experimental unit, and each moth in a vial was a subsample. Therefore, a sample was each trial.

## Sex and Weight

Following each trial, wet weights of moths were recorded, and thereafter moths were euthanized in a −20 °C freezer. Euthanized moths were subsequently dried in a drying oven (KTD-6000, Shyktyo, China) at 42 °C for 48 h and dry weights were recorded. Sex was determined under stereo light microscope (Leica M80, Teaneck, NJ) by visible observation of male cerci or female papilla analis (Drecktrah 1978, Crabo 2018).

## Data Analysis

Statistical analysis was done in R Studio version 4.1 (R Core Team 2022). Summary statistics were conducted to determine mean CTL (minimum and maximum), median, standard deviation, and standard error. Differences between lab-reared and wild-caught samples in each trial type were assessed using linear regression models in base R. We assessed the models for assumptions of violations using the *plot* function. The *ggplot* function in the *tidyverse* package was used to create mean with standard error plots.

A power analysis for Pearson's correlation was conducted using the *pwr.r.test* function from the *pwr* package. Subsequently, Pearson's correlation analyses were performed for each trial group (lab-reared or wild-caught), and each CTL (minimum and maximum). These analyses, conducted using the *cor.test* function in base R, examined the relationship between CTL and the subsample variables wet weight and dry weight.

In the wild-caught moth subsample group, wet-weight was found to be correlated with $CTL_{min.}$ To further explore this relationship, a simple linear regression was performed using the *lm* function in base R. Additionally, a multiple linear regression model was used to assess the combined effects of wet weight and sex on $CTL_{min}$. A 1-way analysis of variance (ANOVA) was also conducted to compare sex with $CTL_{min}$ and $CTL_{max}$ for both lab-reared and wild-caught subsample groups.

For the lab-reared groups, an additional analysis was conducted to evaluate the relationship between CTL and age. Simple linear regression models were performed using the *lm* function in base R.


**Fig. 2.** Critical thermal minimum ($CTL_{min}$) ramping assay. Individual moth vials attached to aluminum sheet shown on top of programmable water bath.

## Results

The CTL (min, max) values for lab-reared and wild-caught *E. auxiliaris* were defined as the mean of the 5 subsamples from each trial. The average $CTL_{max}$ for lab-reared moths across 6 trials was 44.13 °C with a range of 43.72 to 44.56 °C (Fig. 3). The average $CTL_{max}$ for wild-caught moths across 8 trials was 43.28 °C with a range of 42.04 to 44.26 °C (Fig. 3). There was a significant difference in $CTL_{max}$ between lab-reared and wild-caught moths ($R^2 = 0.3531$, adjusted $R^2 = 0.2992$, $F = 6.549$, df = 12, $P = 0.025$).

The average $CTL_{min}$ for lab-reared moths across 8 trials was -2.24 °C with a range from –1.52 to –3.5 °C (Fig. 4). The average $CTL_{min}$ for wild-caught moths across 9 trials was –1.9 °C with a range from –0.5 to –3.38 °C (Fig. 4). There was no difference in $CTL_{min}$ between lab-reared and wild-caught moths ($R^2 = 0.0447$, adjusted $R^2 = –0.0190$, $F = 0.702$, df = 15, $P > 0.1$).

A Pearson's correlation power analysis was conducted with an effect size of $r = 0.5$, power = 0.8, and a significance level of $\alpha = 0.05$. The results of this analysis indicated that subsamples, rather than samples, should be used in subsequent correlation analyses to reduce the likelihood of false positives.

The average wet weight of lab-reared moths (0.2685 g) was 76.74% greater than wild-caught $CTL_{max}$ moths (0.1519 g). The average wet weight of lab-reared $CTL_{min}$ moths (0.2666 g) was 75.51% greater than that of their wild-caught counterparts (0.1519 g). For lab-reared moths, the correlation between wet weight and $CTL_{min}$ was weak, negative, and not statistically significant (Table 1). In contrast, wild-caught moths exhibited a moderately negative and statistically significant correlation between wet weight and $CTL_{min}$ (Table 1).

To further investigate this relationship, a simple linear regression was performed for wild-caught moths, revealing a moderately significant association between wet weight and $CTL_{min}$ ($R^2 = 0.1139$, adjusted $R^2 = 0.0933$, $F = 5.528$, df = 43, $P = 0.0234$). However, the relationship between $CTL_{min}$, sex, and wet weight for wild-caught moths was not significant ($R^2 = 0.1166$, adjusted $R^2 = 0.0519$, $F = 1.804$, df = 41, $P > 0.1$).

The average dry weight of lab-reared $CTL_{min}$ moths (0.1473 g) was 182.6% greater than that of $CTL_{min}$ wild-caught moths (0.0521 g). The correlation between dry weight and $CTL_{min}$ for lab-reared moths was weak and negative, but not statistically significant (Table 1). Similarly, wild-caught moths showed a weak negative correlation between CTL and dry weight, which was also not statistically significant (Table 1).

We observed no significant relationship between CTL and age in lab-reared moths for either $CTL_{min}$ ($R^2 = 0.0319$, adjusted $R^2 = 0.0064$, $F = 1.251$, df = 38, $P > 0.1$) or $CTL_{max}$ ($R^2 = 0.0038$, adjusted $R^2 = -0.0318$, $F = 0.106$, df = 28, $P > 0.1$). Lab-reared moths used in $CTL_{min}$ trials were 3 to 16 d post emergence, with an average age of 8.6 d while those used in $CTL_{max}$ trials were 1 to 11 d post emergence, with an average age of 8.3 d.

For wild-caught moths, there was no significant effect of sex on either $CTL_{min}$ (ANOVA, df = 43, $F = 1.742$, $P > 0.1$) or $CTL_{max}$ (ANOVA, df = 38, $F = 0.677$, $P > 0.1$). Similarly, in lab-reared moths, sex had no effect on $CTL_{min}$ (ANOVA, df = 38, $F = 0.187$, $P > 0.1$) or $CTL_{max}$ (ANOVA,df = 28, $F = 0.228$, $P > 0.1$).

## Discussion

We observed a difference in $CTL_{max}$, with lab-reared individuals demonstrating a higher maximum tolerance compared to their wild-caught counterparts. In contrast, the $CTL_{min}$ values for lab-reared and wild-caught individuals were statistically similar, suggesting a consistent lower limit of thermal tolerance across both groups.

Insects face a great deal of difficulty in adapting to varying climatic conditions and extreme temperatures, as they are dependent on environmental temperatures to regulate body temperature. As

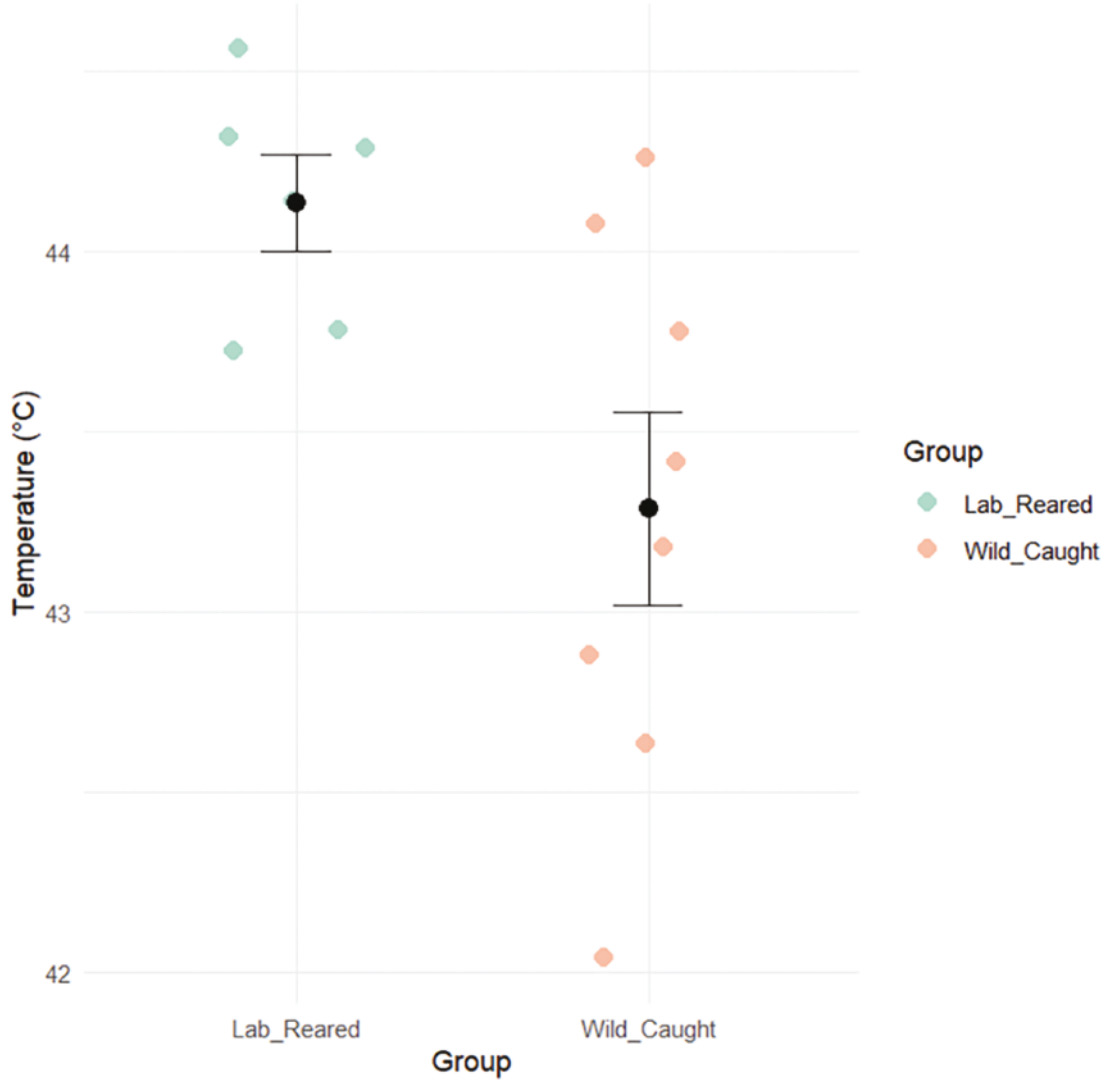


**Fig. 3.** CTLmax averages for lab-reared and wild-caught *Euxoa auxiliaris* adults. Raw data points are shown as jittered dots, with each point representing a trial sample measurement for the respective group (lab-reared or wild-caught). The black dot represents the mean temperature for each group, and error bars indicate the standard error of the mean.

ectotherms, insects are acutely sensitive to temperature fluctuations and rely heavily on physiological and behavioral mechanisms for heat tolerance and thermoregulation (Heinrich 1986, Neven 2000, Hoffmann et al. 2013). Despite these adaptations, most insects are unable to withstand the warmest potential body temperatures and thus lack tolerance to survive extreme heat events (Sunday et al. 2014). To mitigate these challenges, insects utilize various behavioral strategies, such as dispersal behavior and seeking refuge to escape excessive heat (Bale et al. 2002).

Several studies have demonstrated evidence of these thermal adaptations in the CTLs of lepidopteran species. Mutamiswa et al. (2017) compared the thermal tolerances of the crambid *Chilo partellus*, a native Asian species but invasive in similarly hot African climates, to 2 native lepidopteran stem borers. They found that adult *C. partellus* had the highest $CTL_{max}$, 47.81 ± 0.45 °C, indicative of an adaptive relationship between climate and physiological tolerance. These findings suggest that insect species adapted to warmer climates may exhibit greater plasticity when range expansion is enabled by comparatively high $CTL_{max}$ value, reflecting their ability to cope with more extreme temperature conditions. Similarly, Bawa et al. (2021) observed that the $CTL_{max}$ of the Australian populations of the migratory noctuid, *H. punctigera*, was 46.9 ± 0.2 °C in adults and 49.1 ± 0.3 °C in larvae. The results of Bawa et al. (2021), not only highlight the high $CTL_{max}$ values typical of species occupying subtropical and tropical habitats but also indicate that differences in thermal tolerance between life stages may be affected by range distribution and escape behavior. In contrast, lepidopteran species present mainly in cooler regions generally exhibit lower $CTL_{max}$ values. For example, the tortricid *Cydia pomonella* has a $CTL_{max}$ ranging from 42.5 to 44.9 °C, and the sub-Antarctic tineid, *Pringleophaga marioni*, has a $CTL_{max}$ of 38.7 °C (Klok and Chown 1997, Chidawanyika and Terblanche 2011).

These results show that the relationship between habitat climate and thermal tolerance is largely driven by physiological characteristics. However, for migratory species such as *H. punctigera* and *S. frugiperda*, $CTL_{max}$ may be more influenced by their dispersal behaviors, which help them survive in extreme temperatures (Chapman et al. 2015). Correspondingly, *E. auxiliaris*, a species inhabiting temperate climates, has a $CTL_{max}$ consistent with expectations for its cooler habitat, implying a lower thermal tolerance compared to lepidopteran species from warmer regions.

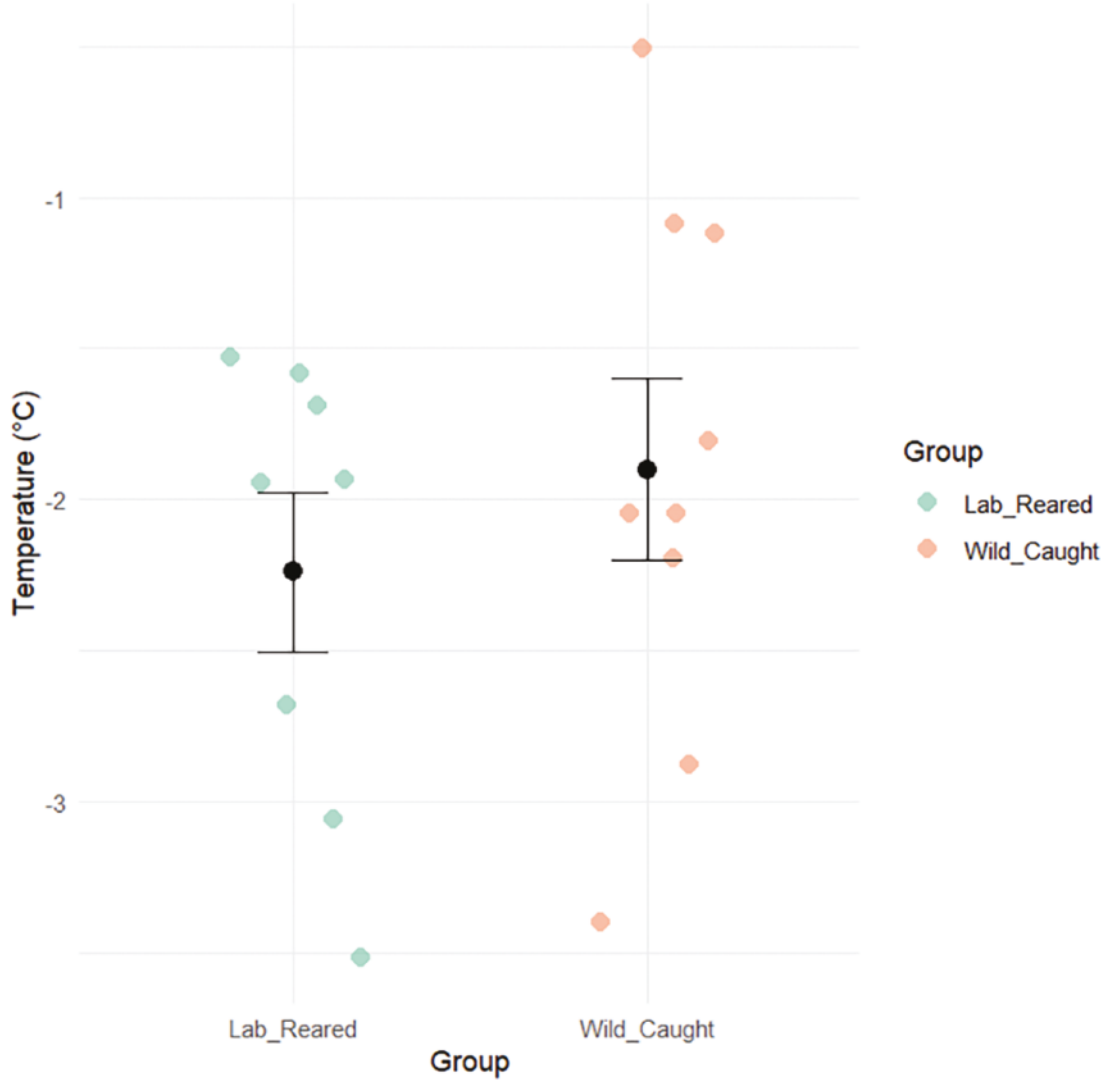


**Fig. 4.** CTLmin averages for lab-reared and wild-caught *Euxoa auxiliaris* adults. Raw data points are shown as jittered dots, with each point representing a trial sample measurement for the respective group (lab-reared or wild-caught). The black dot represents the mean temperature for each group, and error bars indicate the standard error of the mean.

**Table 1.** Pearson's correlation analysis of wet and dry weight with critical thermal limit in lab-reared and wild-caught groups of adult *Euxoa auxiliaris*.

| | | | 95% CI | | | | |
|---|---|---|---|---|---|---|---|
| | | r | Lower | Upper | t | df | P |
| Lab-reared | | | | | | | |
| $CTL_{min}$ | Wet | −0.0626 | −0.3669 | 0.2538 | −0.3868 | 38 | > 0.1 |
| | Dry | −0.1154 | −0.4121 | 0.2034 | −0.7163 | 38 | > 0.1 |
| $CTL_{max}$ | Wet | −0.0408 | −0.3953 | 0.3242 | −0.2163 | 28 | > 0.1 |
| | Dry | 0.1631 | −0.2095 | 0.4943 | 0.8746 | 28 | > 0.1 |
| Wild-caught | | | | | | | |
| $CTL_{min}$ | Wet | −0.3375 | −0.5742 | −0.0488 | −2.3512 | 43 | 0.0233* |
| | Dry | −0.0940 | −0.3771 | 0.2052 | −0.6189 | 43 | > 0.1 |
| $CTL_{max}$ | Wet | −0.1200 | −0.4160 | 0.1989 | −0.7452 | 38 | > 0.1 |
| | Dry | −0.0767 | −0.3792 | 0.2406 | −0.4742 | 38 | > 0.1 |

*Significant relationship at $\alpha = 0.05$.

The influence of temperature on the $CTL_{max}$ of *E. auxiliaris* is further evidenced by the significant difference in $CTL_{max}$ between lab-reared (44.13 °C) and wild-caught moths (43.28 °C). When subjected to different temperature conditions than those to which they are normally adapted, insects can develop physiological resistance to temperature extremes through the process of acclimation

(Terblanche et al. 2011). This adaptive resistance can occur due to natural environmental fluctuations or the specific temperatures experienced during developmental stages (Piyaphongkul et al. 2014, Käfer et al. 2020). For instance, in *Drosophila subobscura*, developmental acclimation plays a crucial role in heat-stress resistance, with individuals reared in warmer conditions demonstrating greater tolerance (Hoffmann et al. 2003, Piyaphongkul et al. 2014).

We collected wild-caught moths in September, which coincides with their remigration to natal ranges for oviposition. These moths experienced a different thermal environment, including a wider temperature gradient and overall lower temperatures compared to their lab-reared counterparts, which were reared from egg to adult at ambient temperatures ranging 22 to 27 °C. These differences in temperature during development likely contributed to the observed variation in $CTL_{max}$ between wild-caught and lab-reared individuals, but determining the influence of acclimation on CTL was beyond the scope of this study. The role of acclimation in *E. auxiliaris* requires further investigation, particularly given the species' extensive natal range, which extends north into Canadian provinces and spans the western side of the Rocky Mountains. This broad distribution suggests that climatic conditions experienced during immature stages could vary considerably across migrating populations (Dittemore et al. 2023). Thus, understanding the effects of these diverse environmental exposures is important for comprehensively assessing the species' thermal tolerance and adaptive responses.

Temperature has long been hypothesized to be a primary factor in the migration of *E. auxiliaris* when Pepper (1932) and Pruess (1963) found decreased longevity of adults correlated with increasing temperature exposure. *Euxoa auxiliaris* spend a substantial portion of their adult life in alpine environments, sheltering from the heat in talus fields during the day and feeding nocturnally on alpine nectar where air temperatures can be below freezing (French et al. 1994, U.S. Geological Survey 2016, Hostetler et al. 2021). These moths return to the Great Plains in the fall to oviposit, where their progeny complete development to emerge as adults in the following spring, confirming this species' ability to withstand cold temperatures throughout all stages of their life cycle.

As with heat tolerance, differences in cold tolerance are commonly correlated with geographic distributions of species (Hoffmann et al. 2003). Considering the alpine environments *E. auxiliaris* occupy, in addition to their heat-averse behaviors and life cycle traits, we expected a $CTL_{min}$ would be reflective of the deployment of a specific mechanism among a suite of available mechanisms for thermoregulation. The influence of microhabitat selection, behavioral mechanisms, and migratory patterns on low thermal tolerance have been documented across various lepidopteran species. These factors affect $CTL_{min}$, illustrating how thermal adaptation plays a role in enhancing fitness and survival. For example, adults of the non-migratory species *C. partellus*, primarily found in the tropical climates of Asia and Africa, exhibit a $CTL_{min}$ of 4.83 ± 0.60 °C (Mutamiswa et al. 2017). Similarly, Keosentse et al. (2021) found that *S. frugiperda*, a species native to tropical regions of the western hemisphere and adapted to exotic habitats, eg southern Africa, has a $CTL_{min}$ of 1.9 ± 0.6 °C. In winter, North American populations of this species migrate to the Gulf of Mexico as they cannot survive winter temperatures because they lack a diapause state, demonstrating an adaptive strategy reflective of their tropical origin (Johnson 1987). In contrast, *C. pomonella*, which inhabit the more temperate regions of North America and Europe, have a $CTL_{min}$ of 0.3 to 1.3 °C. This lower threshold aligns with the cooler environment these species encounter compared to those found in more tropical climates (Chidawanyika and Terblanche 2011). The relationship between $CTL_{min}$ and habitat climate is also evident in *E. auxiliaris*, which have a $CTL_{min}$ of −2.24 °C for lab-reared and −1.9 °C for wild-caught individuals. These values are notably lower than the $CTL_{min}$ of those species adapted to lower latitudes.

This relationship is somewhat expected, given that the motivation for long-distance migration in insects is partially attributed to the avoidance of unfavorable high-temperature conditions in summer and because *E. auxiliaris* historically migrate to cooler conditions than in their Great Plains natal range. However, as discussed with the $CTL_{max}$ of *E. auxiliaris*, the $CTL_{min}$ could also be influenced by environmental adaptations, based on recent research regarding its possible natal range expansion extending farther north into Canada (Dittemore et al. 2023).

Other factors influencing $CTL_{min}$ could be attributed to the effects of migratory behavior. Migration can mitigate environmental stress, but it can also negatively affect metabolic efficiency (Sunday et al. 2014, Shah et al. 2021). Because these movements are highly energy-intensive and costly, they often require suppression of reproductive development in favor of migratory potential (Li et al. 2023). Interestingly, this suppression of reproduction may contribute to greater cold tolerance, as has been observed in cool temperate *Drosophila* species when reproductive suppression was shown to increase cold resistance (Hoffman et al. 2003). Furthermore, to conserve lipids severely depleted during migration, insects such as migratory monarch butterflies, *Danaus plexippus*, select high mountain areas to over summer (Masters et al. 1988). High-altitude areas with cooler temperatures allow them to maintain lower body temperatures, helping to conserve energy reserves and improve overall fitness. These fitness and survival traits are reflected in the life cycle of *E. auxiliaris* which once in the alpine elevations of the Rocky Mountains feed nocturnally on nectar, building up lipid stores that aid in sexual maturation and their return migration to the Great Plains in late summer and early fall (Kendall et al. 1981, White et al. 1998). Considering that these behaviors are illustrative of several mechanisms for thermoregulation, it is possible that our $CTL_{min}$ results are reflective of multiple adaptations.

The exceptionally low $CTL_{min}$ of *E. auxiliaris* stands out compared to other temperate lepidopterans, indicating a strong selection for the cold environments they seasonally inhabit. A low thermal threshold is likely a critical adaptation that allows *E. auxiliaris* to thrive in the harsh conditions of alpine elevations, where they engage in adaptive feeding behaviors. During the night, these moths leave the protective talus slopes where they take shelter during the day and fly to nearby alpine meadows to feed (Kendall et al. 1981, French et al. 1994). The ability to withstand low temperatures is vital, as temperatures at known moth aggregation sites can drop as low as 9 °C to −5.9 °C during the summer months depending on location (Mattson et al. 1991, White et al. 1998, Oregon State University 2024). In support, we have long observed *E. auxiliaris* remaining active at 4 °C during long periods of refrigeration, indicating their capacity to function at low temperatures.

This remarkable thermal tolerance shows the unique adaptations of *E. auxiliaris* to its alpine environment where less cool-tolerant species might be unable to sustain activity. However, although some research has explored the minimum temperature thresholds for flight in temperate migratory noctuids—such as the work by Taylor and Carter (1961), who observed flight cessation at about 8 °C—there is still a need for more detailed research on the nocturnal flight patterns and foraging activities of *E. auxiliaris* in these alpine climates. Understanding these behaviors in greater depth, as well as genetic and physiological adaptations could shed light on how thermal tolerance enables this species to survive and thrive in such challenging conditions.

Unlike our $CTL_{max}$ results, there was no significant difference in the $CTL_{min}$ of lab-reared and wild-caught individuals. These results reflect those of Xing and Zhao (2022), who investigated the effect of developmental acclimation on the thermal tolerance of adult *Plutella xylostella*. They found a significant difference in $CTL_{max}$ across developmental temperatures, but not in $CTL_{min}$, suggesting independence through different regulatory mechanisms. Another possible explanation could be the ability to thermoregulate. During experimental trials, individuals became more active as they approached their $CTL_{min}$ and began shaking and flapping their wings. This behavior is typical of lepidopteran species experiencing low-temperature limits and may explain the closer than expected $CTL_{min}$ between lab and wild individuals (Kammer 1970, Masters et al. 1988).

We did not observe a correlation between age and thermal tolerance for either $CTL_{max}$ or $CTL_{min}$. These findings are contradictory to several studies that have reported age-dependent changes in thermal tolerance both within and across life stages (Toolson and Hadley 1974, Sørensen et al. 2015, Mbande et al. 2023, Mutamiswa et al. 2023). Mbande et al. (2023) in a study on another noctuid, *S. frugiperda,* found that age influenced $CTL_{max}$, with individuals ranging from 3 to 9 d post-emergence. These findings suggest an interaction between age and reproductive maturity in shaping thermal limits in some species. In our study, subsamples for $CTL_{min}$ trials included individuals 3 to 16 d post emergence, while $CTL_{max}$ trials included individuals 1 to 11 d post emergence. Despite this broader age range compared to the range examined by Mbande et al. (2023), we did not detect a correlation between age and CTL. Considering that *S. frugiperda* is multivoltine while *E. auxiliaris* is univoltine, it is plausible that differences in mating status, rather than age alone, may underlie these observations considering that thermal tolerance depends heavily on the population dynamics of a species within a specific environment (Soteres et al. 1984, Bowler and Terblanche 2008, Mbande et al. 2023). The effect of age on thermal tolerance in *E. auxiliaris* has not been investigated, so our findings may not be universally applicable to the species, at least not within the context of our study.

Also, our study did not find a significant correlation between weight (wet or dry) and CTL, except for wet weight in wild-caught moths where $CTL_{min}$ temperature decreased as wet weight increased. This finding may reflect the timing of collection, as wild-caught individuals were likely actively remigrating to natal ranges from alpine summer habitats. Army cutworm moths are believed to mate before reaching natal ranges in the fall, potentially developing eggs during the migratory flight (Pruess 1967, Burton et al. 1980). Reproductive development could influence body mass, consistent with evidence from other species, such as *Pieris napi* and *Cnephasia jactatana,* where body weight correlates with sex and mating status (Jiménez-Pérez and Wang 2004, Almbro and Kullberg 2012).

To explore this further, we tested for an interaction between sex and CTL for each subsample group and sex and wet weight within the wild-caught subsample group but found no significant relationships. However, considering the relationship between thermal tolerance and body mass, reproductive status, and age, it remains unclear whether this result is biologically meaningful. Further investigation would be required to draw definitive conclusions.

The CTL for *E. auxiliaris* was established as the temperature in which moths lost their righting response. This measure is particularly valuable when considering migratory potential. During the annual westward migration, moths may use conducive weather fronts to assist their flight, stopping daily or periodically to feed on nectar sources (O'Koerwitz and Pruess 1964, O'Brien and Lindzey 1998, Kevan and Kendall 1997, White et al. 1998). Remigration to the Great Plains is accomplished with the assistance of the seasonal increase in whole-body lipid content, but available energy stores fall short of migratory distance requirements, suggesting the use of tailwinds to circumvent endogenous limitations and reduce transport costs (White et al. 1998). The impact of shifting weather patterns on migratory potential and patterns is not well understood. An understanding of the thermal limits for species can serve as a starting point for understanding the temperature bounds for flight activity, providing critical insights into how changing temperatures might affect their migratory behavior, including migratory potential and use of stopover sites for replenishing energy stores.

The ability of an insect to maintain activity under thermal stress is a key aspect of its overall fitness (Loeschcke and Hoffmann 2007). This capability directly influences its survival, reproductive success, and ecological interactions. At *E. auxiliaris* aggregation sites in the Rocky Mountains, this principle is particularly evident. During the hyperphagia period preceding hibernation, *E. auxiliaris* act as an accessible and crucial food source for grizzly bears (French et al. 1994). Grizzly bears may consume at least 40,000 moths/day, equaling approximately 20,000 calories (White et al. 1998, Lozano 2022). The success of bear foraging in these areas has been partly attributed to the lethargic state of moths in scree fields due to low-temperature exposure (Mattson et al. 1991). These conditions render the moths an easily accessible and low-energy-expending food source for bears. Understanding $CTL_{min}$ of *E. auxiliaris* is therefore essential for predicting how climatic variation and weather patterns might affect moth escape behavior and availability, which in turn affects bear foraging success and overall ecosystem dynamics.

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Taylor Kennedy (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Funding acquisition [supporting], Investigation [lead], Methodology [lead], Project administration [equal], Resources [equal], Software [lead], Supervision [equal], Validation [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), Sharlene E. Sing (Conceptualization [supporting], Data curation [supporting], Formal analysis [supporting], Funding acquisition [equal], Investigation [supporting], Methodology [supporting], Project administration [equal], Resources [equal], Software [supporting], Supervision [supporting], Validation [supporting], Visualization [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), and Robert Peterson (Conceptualization [equal], Data curation [supporting], Formal analysis [supporting], Funding acquisition [lead], Investigation [equal], Methodology [equal], Project administration [lead], Resources [lead], Software [supporting], Supervision [lead], Validation [supporting], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal])

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*Conflicts of interest*. The authors declare no conflict of interest.

## Data Availability

Data are available upon request to the corresponding author.

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