



The effects of temperature and barometric pressure on the wingbeat frequency of the seasonal migrant, *Euxoa auxiliaris* (Lepidoptera: Noctuidae)

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The annual westward migration of army cutworm moths, *Euxoa auxiliaris* (Grote), to the Rocky Mountains plays a crucial role in the diet of grizzly bears, *Ursus arctos horribilis* (L.), which face considerable variability in food availability throughout the year. During the bears' hyperphagia period, when they must consume an excess of calories to prepare for hibernation, these migrating moths provide a vital and reliable energy source. Seasonal dispersal of *E. auxiliaris* has been primarily documented through ground observations. However, advancements in radar technology now offer new opportunities to track high-altitude migrations including direction, speed, and wingbeat frequency (WBF) of flying insects. Atmospheric conditions such as temperature and pressure can influence insect flight dynamics, yet their effects on *E. auxiliaris* remain poorly understood. Therefore, we characterized the WBF of lab-reared *E. auxiliaris* under 9 combinations of air temperature (7, 13, 24 °C) and pressure (550, 700, 850 hPa). Using a pressure-controlled altitude chamber, individual moths were systematically subjected to combinations of these conditions, and their WBFs were recorded. Our results show that temperature significantly affected WBF, but barometric pressure did not. These findings provide critical baseline data for understanding the flight dynamics of *E. auxiliaris* and highlight the importance of integrating biological data into radar-based studies of migration. These results enhance the interpretation and utility of radar-derived datasets and contribute to the development of more accurate monitoring tools, particularly for the study of insect migration.

Keywords: army cutworm, Rocky Mountains, Great Plains, flight dynamics, migration

Introduction

Ongoing expansion of croplands coupled with low levels of protected, interconnected wild lands in North America, requires migratory movements of organisms to act as essential links between distant and diverse habitats (Templeton et al. 2001, Lobell et al. 2002, Hanski and Pöyry 2007, Saura et al. 2017, Lark et al. 2020). By transporting nutrients, organisms, and pathogens, migrations facilitate dynamic exchanges that influence the ecosystems that they temporarily occupy (Bauer and Hoyer 2014). These movements not only shape the structure of the ecosystems they pass through but they also affect species abundance and diversity therein (Bauer and Hoyer 2014).

One such migratory species is the army cutworm moth, *Euxoa auxiliaris* (Grote, Lepidoptera: Noctuidae), which plays a key role in these ecological connections. Ranging from Canada to the Great Plains to the Rocky Mountains, the larvae are an agricultural pest, feeding on a wide variety of cultivated crops (Wilcox 1898, Walkden 1950, Burton et al. 1980, White et al. 1998, Dittmore et al. 2023). Yet in their adult migratory stage, these moths serve as a critical food source for grizzly bears, *Ursus*

arctos horribilis (L., Carnivora: Ursidae) (Mattson and Reid 1991, Mattson et al. 1991, O'Brien and Lindzey 1998).

Each spring, *E. auxiliaris* embark on a westward migration to the Rocky Mountains, likely driven by the need to escape high summer temperatures and limited nectar resources in their natal Great Plains habitats (Pruess 1967, Hardwick and Lefkovich 1971, Burton et al. 1980). Once in the alpine environments of the Rocky Mountains, *E. auxiliaris* feeds nocturnally on nectar and shelters in talus fields during the day (Pruess 1967, Burton et al. 1980, French et al. 1994). These seasonal aggregations serve as a high-calorie, easily accessible food source for grizzly bears, especially during hyperphagia when the bears' energy demands are heightened (French et al. 1994).

The capacity for long-distance migration by *E. auxiliaris* is supported by Koerwitz and Pruess (1964), whose flight-mill studies confirmed the moth's ability to sustain extended flight when fueled by food reserves and aided by favorable environmental conditions. These findings suggested that during migration, moths likely use conducive weather fronts to aid flight and nectar feeding during restorative stopovers to replenish

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energy stores (Kevan and Kendall 1997, White et al. 1998). Pruess (1967) documented field evidence of a westward migration of *E. auxiliaris* through light trap collections from Nebraska to Wyoming, suggesting these movements occurred from the Great Plains to the Rocky Mountains. More recent research linked moths located at aggregation sites in the Rocky Mountains back to their natal origins through stable isotope analysis, offering a clearer picture of their migration routes, including evidence of natal ranges extending to Canada and the western slopes of the Rocky Mountains (Dittemore et al. 2023).

Although research on insect migration has often focused on establishing movement patterns, technological advances such as radar monitoring have greatly improved our ability to track migrating insect populations (Beerwinkle et al. 1994, Chapman et al. 2003, Chapman et al. 2011). Radar can provide insights into the wingbeat frequency (WBF), body mass, shape, and orientation of target signals during flight (Chapman et al. 2003). However, these radar-derived variables result in ambiguous species identification without direct confirmation, which can be difficult to accomplish at altitudes where mass-movement events often occur. Therefore, to support target attribution, species-specific laboratory studies may allow for more accurate predictions of numbers, biomass, and calorie-flux in and out of the habitats migrating insects seasonally inhabit.

One of the radar-derived variables, WBF, can be particularly valuable in species-specific target attribution. As a critical flight parameter, WBF plays a major role in determining an insect's performance by influencing the generation of force, lift, and speed (Dickinson et al. 1999, Ellington 1999, Taylor 2001). These frequencies can vary widely across species, driven by factors like body mass and wing size (Ellington 1999). Body mass often correlates with taxonomic grouping, with most of the variation occurring at the genus and species level (Chown and Gaston 2010). Yet, despite this, studies often report WBF at the broader family level, leaving room for a more nuanced understanding. For example, Yu et al. (2020) documented WBF ranges between 16.48 and 60.83 Hz for some species in Noctuidae, although Lapshin and Vorontsov (2007) found that the noctuids they studied had a WBF range of 30 to 50 Hz.

To better understand the migratory potential and patterns of *E. auxiliaris*, it is essential to determine species-specific WBF and primary environmental factors influencing migratory behavior. This knowledge will provide key insights into flight dynamics and improve the accuracy of remote-sensing methods for target attribution, given the inherent challenges of identifying species from radar data.

E. auxiliaris flies at varying temperatures and altitudes, with altitude directly correlated to atmospheric pressure (Pruess and Pruess 1971, West 1996). Therefore, we examined the influence of temperature and barometric pressure on WBF in lab-reared *E. auxiliaris* individuals. Considering the relationship between temperature and altitude, we hypothesized that variations in both factors would affect WBF, anticipating that changes in environmental conditions would concurrently alter the flight dynamics of migrating moths (West 1996).

Methods and Materials

Wild Population Collection

In August 2023, live adult *E. auxiliaris* were nondestructively collected using pheromone traps baited with Scentry Army Cutworm Lures 12/CS (Scentry Biologicals Inc., Billings,

Montana, United States) in Powell, Wyoming, United States, and from a blacklight trap (#2851A Universal Collecting System, BioQuip Products, Inc., Rancho Dominguez, California, United States) in Bozeman, Montana, United States. Moths were kept at ambient temperatures during transport and when returned to the laboratory, moved to mesh-screened metal rearing cages (BioQuip Products, Inc., Rancho Dominguez, California, United States) for oviposition. Each cage housed 20 to 30 moths and was lined with paper towels for shelter. The moths were retained at ambient temperature (22 to 27 °C) and fed daily via cotton balls moistened with a 10% sucrose solution. To provide a suitable substrate for oviposition, an 85-mm diameter petri dish filled with steam-sanitized soil that had been sifted through 8-gauge wire mesh was placed in the bottom of each cage. Egg presence in those petri dishes was monitored daily using a stereo microscope (Leica M80, Teaneck, New Jersey, United States). Once eggs were detected, the petri dishes were moved into vented plastic containers and stored in complete darkness at ambient temperatures of 22 to 27 °C until hatching occurred.

Laboratory Population Culture

E. auxiliaris larvae were reared at ambient temperatures (22 to 27 °C) and 60% relative humidity (e_a/e_{sat} , kPa/kPa, RH), with a 12:12 light–dark photoperiod. They were fed a multiple species diet (Southland Products Inc., Lake Village, Arkansas, United States) dispensed in 30-mL deli cups with perforated lids. The diet was replaced every 4 to 6 days, depending on feeding frequency and condition of diet. Pupation took place within the diet cup, and the pupae were left undisturbed for 3 to 4 days to reduce harm from handling newly formed pupae. After this period, pupae were carefully transferred from individual diet cups into ventilated 5.7-L plastic containers lined with paper towels. Each container stored approximately 25 to 35 pupae, which were kept in total darkness at ambient temperatures (22 to 27 °C). The paper towels were misted with deionized water every other day to ensure adequate moisture for the developing pupae. Once the pupae showed sufficient darkening, they were relocated to the bottom of a rearing cage to provide a suitable environment for eclosion. Moths emerged between October 30 and November 15, 2023, and were kept in the same light and temperature conditions as the larvae until they were used for experiments from November 28 to December 19, 2023.

Experimental Variables

Experiments were conducted under fixed effects of varying barometric pressure (550, 700, and 850 hPa) combined with different temperature treatments (7, 13, and 24 °C). These combinations were designed to simulate the environmental conditions likely experienced by migrating *E. auxiliaris*. Although the effect of sex on WBF was not specifically investigated, sex was determined for 163 of the total 191 individuals tested, yielding a ratio of 75 females to 88 males.

Experimental Design

Individual moths were considered the experimental unit and were randomly assigned to each of the 9 possible temperature and pressure treatment combinations. A power analysis was conducted and each treatment group was assigned a sample size of $n=20$ to 25. WBFs were measured inside a 45-cm × 45-cm × 45-cm pressure-controlled altitude chamber (Custom, Sanatron Inc., Salt Lake City, Utah, United States). The

chamber was equipped with a vacuum controller (Sanatron Inc., Salt Lake City, Utah, United States), allowing precise manipulation of internal pressure. To achieve temperature control within the chamber, a repurposed transmission oil cooler (Hayden Ultra-Cool Transmission Oil Cooler-403, O'Reilly Auto Parts, Bozeman, Montana, United States) was integrated with a liquid feed-through connected to an external thermoelectric cooling unit (F-25MC, JULABO, Germany). The transmission oil cooler was housed inside a Styrofoam cooler, improving temperature stability within the vacuum chamber. Temperature was measured continuously using a digital thermometer (ThermoPro TP50, Atlanta, Georgia, United States). For acoustic WBF recording, a piezoelectric microphone (ICP Microphone System, 378A06, PCB Piezotronics, Depew, New York, United States) was placed on top of the transmission oil cooler next to a wall-mounted toggle serving as a perch for test subjects (Fig. 1) (Lapshin and Vorontsov 2007).

To prepare each moth for WBF measurement, a strip of construction paper was attached with superglue (Loctite, Westlake, Ohio, United States) to the ventral side of the abdomen, just below the thoracic–abdominal junction. Once secure, the strip was carefully removed, which also removed scales from the moth's integument. A clean strip was then firmly affixed to the abdomen. The attached paper strip was taped to a 3-D printed mount positioned behind the wall-mounted toggle on which the moth stood (Fig. 2). The entire setup was enclosed inside the Styrofoam cooler. Once the chamber was sealed and brought to pressure (taking 30 to 60 s), the toggle was dropped from under the standing moth to stimulate natural flight. WBF typically increased and then stabilized after stimulation. We visually monitored this process until rhythmic flight was established, then the piezoelectric microphone was turned on and

WBF was recorded. The recording was facilitated by a data acquisition system (cDAQ-9174, NI, Austin, Texas, United States) and an Integrated Electronics Piezo-Electric module (NI-9230, NI, Austin, Texas, United States). In cases where multiple recordings were made, the recording with the least spectral noise was selected for analysis. Data were recorded at a rate of 3.2 kHz. Signal durations averaged 48.6 ± 16 s (mean $\pm$ SD). During the experimental trial period, all aspects of the setup were determined at random, the temperature–pressure combinations and the number of trials conducted that day were determined by a random number generator, and individual moths were randomly chosen by hand from a rearing cage containing 75 to 100 moths without any preference for the individual removed.

Data Analysis

All data were postprocessed in MATLAB R2023B. To determine WBF, we converted the time series to the frequency domain via a Fast Fourier Transform (FFT) function. Time-series data were zero padded to the next power of 2 (eg a signal of 115,200 samples is padded with zeros to achieve a signal length of $2^{17} = 131,072$ samples). No windowing was applied to the time-series data. The frequency resolution of the transformed signal was $16 \text{ mHz} \pm 7 \text{ mHz}$ (mean $\pm$ SD). We subsequently calculated the frequency response magnitude from the complex FFT. We applied a moving mean filter with 100 samples to the frequency response magnitude. This filter length was selected empirically to suppress spectral noise while preserving the dominant peak associated with the WBF. We then used an intrinsic MATLAB peak finding algorithm, *findpeaks*, with a minimum peak width of 45 samples, to identify the frequency that corresponded to the maximum sound pressure level recorded via the piezoelectric

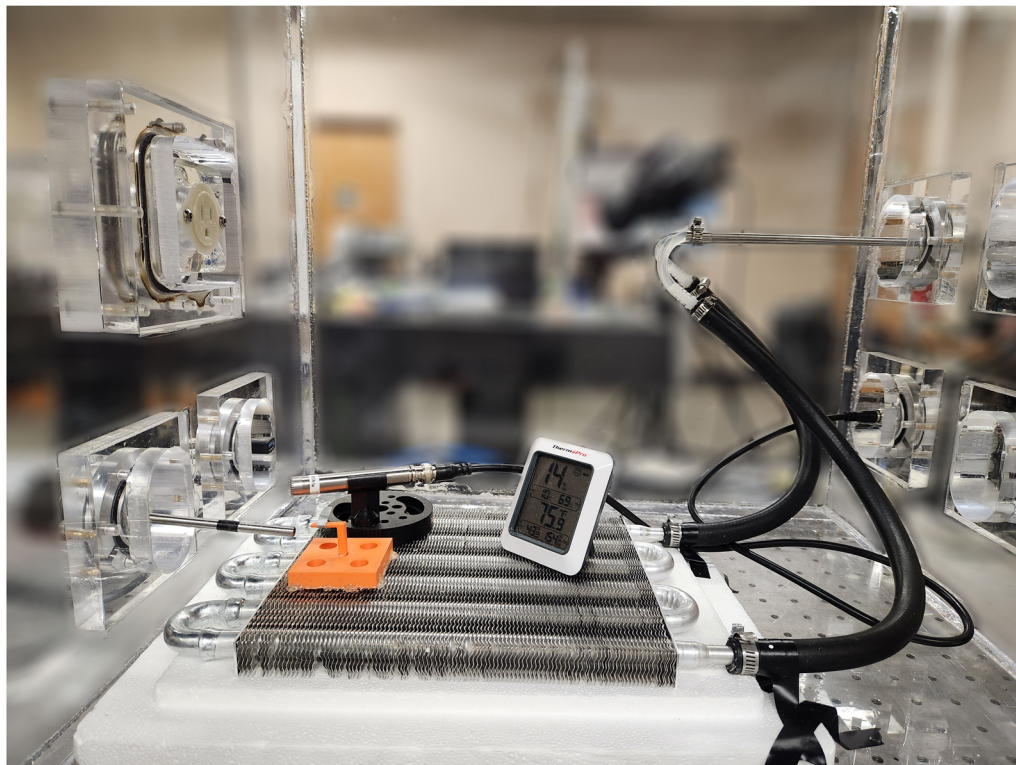


Fig. 1. Experimental setup for wingbeat frequency (WBF) experiments. A chamber wall-mounted toggle sits left of an orange 3D-printed stand where the moth will be attached. A piezoelectric microphone is positioned next to the toggle to record WBF. Underneath is the repurposed transmission cooling plate and the lid to the styrofoam cooler. Equipment is enclosed in a cooler for WBF recording. Photo: T.E. Kennedy.



Fig. 2. *Euxoa auxiliaris* moth flying above a wall-mounted toggle, held stationary by a strip of paper affixed to the abdomen and taped to a 3D-printed stand. To the right of the moth is the piezoelectric microphone for wingbeat frequency recordings. Photo: T.E. Kennedy.

microphone. This width corresponds to about 0.72 Hz based on our mean frequency resolution and was selected to distinguish the WBF peak from nearby noise artifacts. We assumed this frequency corresponded to the insect's WBF.

Statistics

Statistical analysis was conducted in R Studio version 4.1 (R Core Team 2022). Normality of WBF within each temperature–pressure group was assessed using histograms and *Q–Q* plots using the *ggplot* function in the *ggplot2* package. The Shapiro–Wilk test for normality was conducted for each treatment group using the *shapiro-test* function from the *stats* package in base R. Since 2 groups exhibited nonnormality, Levene's test for homogeneity of variances was performed using *leveneTest* function from the *car* package which confirmed homogeneity.

We proceeded with a 2-way ANOVA using the *aov* function from the base R *stats* package, incorporating main effects and their interaction term. Tukey's Honest Significant Difference (HSD) test was carried out using the *TukeyHSD* function from the “stats” package to conduct post hoc comparisons (McHugh 2011).

Boxplots and violin plots for WBF and temperature and pressure were created using the *ggplot* function in the *ggplot2* package. To ensure accessibility, colorblind-friendly palettes from the *RColorBrewer* package were applied.

Results and Discussion

The mean WBF of *E. auxiliaris* across all trials was 37.07 Hz, with individual frequencies from 23.03 to 49.94 Hz. This WBF value was the overall mean across all 191 individuals, each subjected to 1 of 9 temperature-by-pressure experimental treatments. These data illustrate substantial variation in WBF, reflecting the influence of variability in specific environmental conditions on individual performance.

In our investigation of *E. auxiliaris* WBF, a 2-way ANOVA was conducted to assess the effects of temperature and barometric pressure on WBF. Pressure did not significantly influence WBF (ANOVA, $F_{2,182} = 1.782$, $P > 0.1$), although temperature did (ANOVA, $F_{2,182} = 25.156$, $P < 0.001$) (Table 1). The ex ante expectation that WBF would be affected by a correlation between temperature and barometric pressure was not statistically supported as no significant interaction was found between these 2 variables (ANOVA, $F_{4,182} = 1.677$, $P > 0.1$) (Table 1). This suggests that temperature is a driver for variation in WBF, while pressure, either independently or through interaction with temperature, may not exert a measurable influence on WBF. The link between temperature and WBF in Lepidoptera is well documented. In *Manduca sexta* (L.), Stevenson and Josephson (1990) found that increased temperatures enhanced flight muscle contraction, leading to a higher WBF. Similarly, tethered flight studies of the migratory noctuid, *Mythimna separata* (Walker), revealed that WBF increased as temperatures rose 8 to 24 °C, highlighting the thermal effects on flight mechanics (Xu et al. 2023). Field studies of male *Choristoneura fumiferana* (Clemens) also paralleled these findings (Régnière et al. 2019a, 2019b). Our results are similar to these observations, as *E. auxiliaris* demonstrated a clear temperature-dependent change in WBF, increasing as temperature increased with a mean WBF of 35.08 Hz at 7 °C, 37.94 Hz at 13 °C, and 40.42 Hz at 24 °C (Fig. 3). Pairwise comparisons revealed significant differences between 7 and 13 °C (mean difference = 2.86 Hz, 95% CI [1.0447 to 4.6735], Tukey's HSD, $P < 0.001$), 24 and 7 °C (mean difference = 5.34 Hz, 95% CI [3.5016 to 7.1773], Tukey's HSD, $P < 0.001$), and 24 and 13 °C (mean difference = 2.48 Hz, 95% CI [0.6087 to 4.3521], Tukey's HSD, $P = 0.006$) (Fig. 3).

Temperature is a powerful driver in insect flight physiology, shaping critical metabolic and muscular processes that fuel flight (Acar et al. 2001, Colinet et al. 2015, Léger et al. 2024).

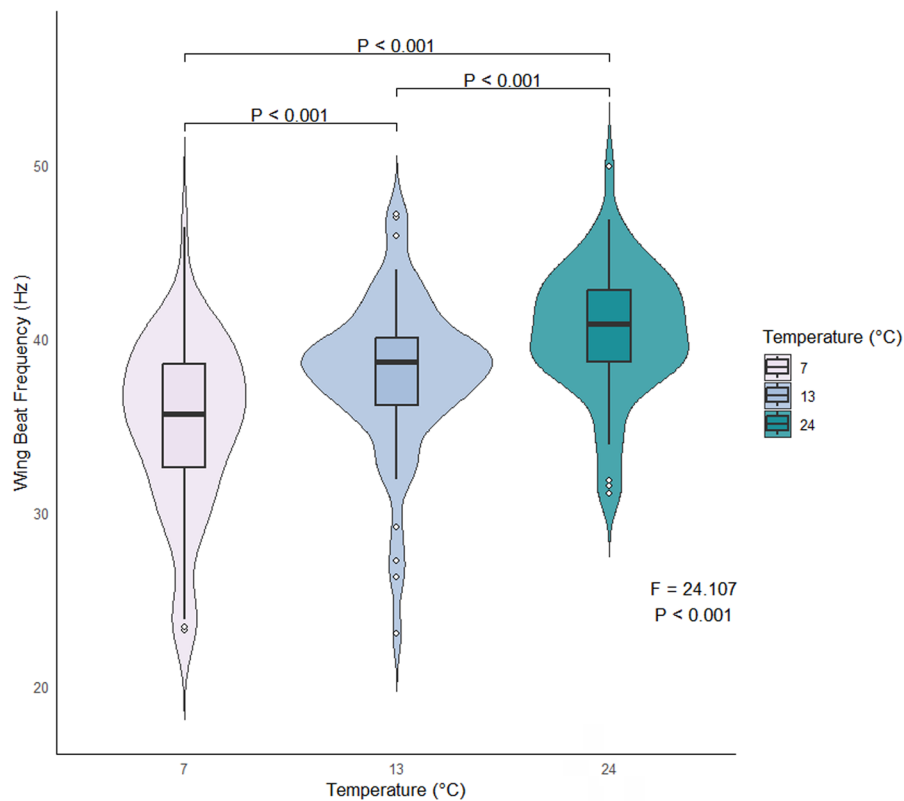


Fig. 3. Violin plot showing the distribution of WBF across 3 temperature treatments (7, 13, and 24 °C). The violins illustrate the smoothed density of the data, while the boxplots inside each violin represent the interquartile range and median WBF. Brackets above the violins indicate significant comparisons between temperature treatments, with $P < 0.001$ for all comparisons.

Table 1. Two-way ANOVA of temperature and pressure on wingbeat frequency (WBF) of *Euxoa auxiliaris*

	SS	df	MS	F	P
Temperature	914	2	457.1	24.11	<0.001 ^a
Pressure	73	2	36.6	1.93	>0.1
Temperature × Pressure	112	4	28	1.47	>0.1
Residuals	3,451	182	19		

^aSignificant relationship at $\alpha = 0.05$.

Among these processes, the mobilization of carbohydrate and lipid reserves plays a pivotal role, providing the necessary energy to initiate and sustain long-distance movements (Arrese and Soulages 2010). Additionally, as temperatures increase, so does the rate of flight muscle contractions, in turn affecting an insect's WBF (Heinrich 1981).

This thermal relationship with WBF aligns with what we know about moth migration. Many migratory moths are known to fly at altitudes of several hundred meters where they encounter temperatures typically higher than their minimum thresholds for flight (Chapman et al. 2002, Wood et al. 2006, Feng et al. 2009). Their concentration at these altitudes is intentional, as warm layers in the atmosphere provide ideal conditions for long-distance travel, allowing migratory moths to conserve energy while covering great distances (Chapman et al. 2011, Reynolds et al. 2017). For example, noctuid moths concentrate in the atmospheric boundary layer where air temperatures range 12 to 16 °C, temperatures higher than their known lower threshold (Wood et al. 2006). Similarly, *C. fumiferana* favor warmer air for long-distance transport (Régnière et al. 2019).

These findings support that rather than being constrained by low temperatures, these moths may seek out altitude layers that allow for optimal flight conditions, potentially enhancing migratory efficiency.

Unsurprisingly, low temperatures have the opposite effect on insect flight, decreasing WBF as temperature drops. The minimum temperature thresholds for flight can vary across species, although, in some temperate noctuids flight ceases at approximately 8 °C (Taylor and Carter 1961). In our study, *E. auxiliaris* flew at temperatures as low as 7 °C. Since individual moths were only exposed to temperature treatments for 2 to 5 min, our methods may not have fully captured the impact of prolonged cold exposure on flight cessation. However, given that the species' critical thermal minimum, defined by loss of righting response, is as low as −3.5 °C, *E. auxiliaris* likely retains the capacity for flight at very low temperatures (Kennedy et al. 2025). In addition, we have observed that *E. auxiliaris* moths remain active at 4 °C during long periods of refrigeration, and they can fly at that temperature.

Given the essential role of atmospheric conditions in flight optimization, we may expect barometric pressure shifts—caused by changes in altitude—to influence the WBF of migratory insects, whose journeys take them through layers of varying pressures (Brombacher 1944, West 1996, Feng et al. 2009). However, our findings did not reveal a statistically significant relationship between barometric pressure and the WBF of *E. auxiliaris*, suggesting that these moths may possess adaptations that maintain consistent flight performance across pressure gradients. This stability in WBF aligns with findings in the migratory moth, *M. separata*, which also showed no significant WBF changes when exposed to barometric pressures 653 to 1013 hPa

(Xu et al. 2023), which is similar to the range of our study treatments of 550, 700, and 850 hPa. The similarity in results across these and additional studies suggests an adaptation in migratory moths to maintain wingbeat frequencies across fluctuating pressures, allowing them to function effectively at varying altitudes encountered during migration.

The ability to stabilize WBF across pressure gradients is particularly advantageous when considering the influence of wind on insect migration. Wind plays an important role in optimizing migratory flight, shaping altitude selection, energy efficiency and success of long-distance travel. Migratory species often take advantage of favorable wind patterns, concentrating at altitudes with the fastest preferred directional wind speeds (Chapman et al. 2008, Alerstam et al. 2011, Chapman et al. 2016, Reynolds et al. 2017). The migratory noctuid *Autographa gamma* (L.) takes advantage of strong tailwinds, traveling at altitudes where wind speeds exceed flight speed, thereby conserving energy and reducing transportation costs (Alerstam et al. 2011). *E. auxiliaris* may be able to respond quickly to shifts in wind because wind resistance decreases migration altitudes, suggesting a sensitivity to unfavorable wind conditions (Pruess and Pruess 1971, Casey et al. 2025). However, the effects of wind assistance on flight and more specifically their WBF remain unknown. Understanding how *E. auxiliaris* might leverage supportive winds to maintain or even optimize WBF could provide deeper insights into how they adaptively adjust their flight mechanics for efficient, long-distance travel.

These investigations into how abiotic factors like temperature and barometric pressure influence WBF of *E. auxiliaris* can contribute to the attributional accuracy of radar-based studies of this migratory species. In more recent years, radar technology has become an effective tool for measuring and characterizing aerial features of insect migration, offering key insights into flight orientation, stratification, wingbeat frequency, and broader aspects of migratory behavior (Beerwinkle et al. 1994, Chapman et al. 2003, Westbrook 2008). Given that migratory behaviors and flight characteristics are closely shaped by atmospheric conditions, a better understanding of how temperature and barometric pressure affect the WBF of *E. auxiliaris* may improve the precision of radar-based species identification and monitoring (Alerstam et al. 2011, Chapman et al. 2011).

With refined radar data on *E. auxiliaris*, researchers may be able to more accurately estimate this species' numbers, biomass, and calorie contributions to the ecosystems they seasonally inhabit. Such insights hold value for conservation and management efforts to maintain grizzly bear populations, which rely on *E. auxiliaris* as a high-energy seasonal food source (French et al. 1994).

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Author Contributions

Taylor E. Kennedy (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Investigation [lead], Methodology [equal], Project administration [lead], Resources

[supporting], Software [equal], Supervision [lead], Validation [lead], Visualization [equal], Writing—original draft [lead], Writing—review & editing [lead]), Mark A. Jankauski (Conceptualization [equal], Data curation [supporting], Formal analysis [equal], Methodology [equal], Resources [equal], Software [equal], Supervision [supporting], Validation [equal], Writing—review & editing [equal]), Jenna McNally (Methodology [supporting], Software [supporting]), Sharlene E. Sing (Funding acquisition [equal], Project administration [supporting], Resources [equal], Writing—review & editing [equal]), and Robert K.D. Peterson (Conceptualization [equal], Funding acquisition [lead], Project administration [equal], Resources [lead], Supervision [equal], Visualization [equal], Writing—review & editing [equal])

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Conflicts of Interest

The authors declare no conflict of interest.

Data Availability

Data are available on request to the corresponding author.

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