CONNECTING BIOREGIONS: MIGRATION OF THE ARMY CUTWORM MOTH (EUXOA AUXILIARIS, LEPIDOPTERA: NOCTUIDAE)

by

Taylor Elizabeth Kennedy

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Entomology

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2025

DEDICATION

This thesis is dedicated to my dog Zara. Thank you for being the light along the way. I would not have been able to do this without you.

ACKNOWLEDGEMENTS

First and foremost, I would like to express my sincere gratitude to the United States Department of Agriculture and the Forest Service Rocky Mountain Research Station for funding this research. Thank you to Andrew Pils, Kerry Murphy, Dan Tyers, and Doug Johnson at the Forest Service and Dean Follett at Clark's Fork Fish Hatchery for your invaluable logistical and field support, your contributions were instrumental to the success of this project. I would also like to thank Montana State University, Department of Land Resources and Environmental Sciences for providing additional resources and institutional support throughout the course of my graduate work. To my advisor, Dr. Bob Peterson, thank you for your guidance, encouragement, support, and most importantly for believing in me. I would not be here without you. I am also deeply grateful to Dr. Tracy Sterling for your continued encouragement, and to Dr. Sharlene Sing for generously sharing your expertise and offering key support during this project. A special thanks to Dr. Robb Diehl for your mentorship, knowledge, equipment and unwavering commitment, this project would not have been possible without you. Many thanks to Dr. Mark Jankauski for your mechanical engineering expertise and to your lab members, Jenna McNally, Cailin Casey, and Braden Cote for technical assistance. I would also like to acknowledge Jordan Rainey, Marni Rolson, and Jackson Strand for their assistance with insect rearing. Thank you to Alieda Stone and Tom Helm at Seed Source Inc. for your generous scholarship support. And to my friends and family, thank you for your love and encouragement throughout this journey, and to Meagan Schmidt for supporting my personal growth. And finally, to my dog Zara–thank you for being my faithful companion and constant source of comfort through it all.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES CONTINUED

ABSTRACT

Each summer, *Euxoa auxiliaris* (Grote) migrate from the agricultural lowlands of North America to high-elevation habitats in the Rocky Mountains, where they aggregate in talus fields during the day and forage on alpine flowers by night until returning to natal ranges at the end of the season. During this period, these moths provide a high-calorie food source for the grizzly bear, *Ursus arctos horribilis* (Linnaeus, Carnivora: Ursidae), which relies on this resource to build essential fat stores for hibernation. Despite the ecological importance of *E. auxiliaris* within these mountain ecosystems, limitations in ground-based observations have restricted our understanding of their role, leaving key knowledge gaps in both grizzly bear management and broader alpine ecosystem dynamics. Improving our understanding of *E. auxiliaris* migration is essential not only for the conservation of grizzly bears in the Rocky Mountains, but also for recognizing the functional linkages between geographically disparate ecosystems. To address this, we investigated the physiological and behavioral characteristics of *E. auxiliaris*, including critical thermal limits and wingbeat frequency under environmental stress, and used radar to track migratory patterns in the Greater Yellowstone Ecosystem (GYE), aiming to predict the timing and magnitude of moth arrivals into seasonally occupied alpine habitats. We determined the critical thermal limits (CTL_{max} and CTL_{min}) of both lab-reared and wild-caught moths, finding a CTL_{max} typical for a temperate lepidopteran species, but a CTL_{min} that reflected an extraordinary ability to remain active and feed under cold conditions. Wingbeat frequency was measured under controlled combinations of temperature and barometric pressure, and our results show that temperature significantly affected wingbeat frequency, but barometric pressure did not. Radar monitoring over two years and across two sites revealed consistent migratory trajectories that delivered millions of moths and thus millions of calories into alpine zones of the GYE. These findings demonstrate the value of radar for characterizing the movement ecology of *E. auxiliaris*, highlights the physiological resistance that enables migration, and underscores the ecological importance of this insect to the persistence of grizzly bears in the Rocky Mountains.

CHAPTER ONE

LITERATURE REVIEW

Introduction

The army cutworm moth, *Euxoa auxiliaris* (Grote; Lepidoptera: Noctuidae), is a migratory noctuid with a range that spans the Great Plains to the Rocky Mountains (Burton et al. 1980, White et al. 1998b). Named for its behavioral resemblance to the true armyworm (*Mythimna unipuncta*), *E. auxiliaris* larvae feed on a wide variety of cultivated plant and weedy plant species, moving collectively to adjacent fields once a food source is depleted (Wilcox 1898). Upon emergence as adults, *E. auxiliaris* migrates to the Rocky Mountains following the spring bloom upward in elevation, spending the summer months in alpine environments feeding nocturnally on nectar and aggregating in talus crevices during the day (Pruess 1967, Burton et al. 1980, French et al. 1994). These seasonal aggregations provide a high-caloric food source for grizzly bears (*Ursus arctos horribilis*), particularly in the Greater Yellowstone Ecosystem (GYE), where they play a crucial role in bear foraging during hyperphagia (French et al. 1994).

Although the seasonal presence of *E. auxiliaris* in the Rocky Mountains is well documented, the origins of these alpine populations were less understood until recently (Kendall et al. 1981, French et al. 1994, White et al. 1998b, Robison et al. 2006, Dittemore et al. 2023). The natal range of *E. auxiliaris* has long been primarily associated with the Great Plains, where larvae have agricultural impacts (Walkden 1950, Pruess 1961, Pruess 1967, Burton et al. 1980, Michaud et al. 2006). However, observations of larvae west of the Rocky Mountains and as far north as Canada supports a broader geographic distribution (Snow 1925, Floate and Hervet

2017). Despite these records, the migratory connection between natal ranges and alpine aggregation sites remained largely speculative until recently. Advances in stable isotope analysis have provided direct evidence that alpine-collected *E. auxiliaris* originate from natal sites spanning both sides of the Rocky Mountains and extending into Canada (Dittemore et al. 2023). This discovery challenges the long-held assumption of a primarily east-to-west migration pattern and underscores the complexity of their movement ecology. Understanding these migratory linkages is crucial for establishing long-term population dynamics, and it provides insights into the environmental factors influencing their abundance, distribution, and availability for alpine predators, including grizzly bears in the GYE.

Euxoa auxiliaris Life History

In the Great Plains, female moths preferentially oviposit during autumn nights, laying as many as 1,000–2,500 eggs directly into the loosely turned soil of crop fields (Jacobson and Blakeley 1959, Drecktrah 1978, Burton et al. 1980). Reproductive success is closely tied to environmental conditions, particularly temperature, which directly affects both oviposition rates and overall fecundity. Temperature influences egg-laying behavior, limiting oviposition at low temperatures (0 °C) and increasing it at higher temperatures (21 °C), thereby shaping total reproductive output for individuals (Cooley 1916, Pruess 1963). Embryonic development is rapid, with most larvae emerging within six days (Jacobson and Blakeley 1959, Burton et al. 1980). Neonates feed on the foliage of host plants at night and remain quiescent during the day (Jacobson and Blakeley 1959, Floate and Hervet. 2017).

The larvae will typically feed until the second instar and then enter a period of dormancy during the winter months. Larvae overwinter in the soil before resuming feeding in the spring and progressing toward pupation (Burton et al. 1980). Pupation occurs after the sixth or seventh instar is reached; at this stage, larvae burrow into the soil and construct an earthen pupal cell, with the anterior end vertically oriented to the soil surface (Cooley 1916, Snow 1925, personal observation 2022).

Abiotic factors such as precipitation and temperature influence egg and larval development at multiple stages. While rearing army cutworms, Cooley (1916) observed that sufficient moisture was essential for successful egg hatch, as embryos were unable to split the egg chorion when conditions were too dry. Moisture availability continues to affect larval and pupal development, as desiccation threatens larvae in dry conditions, while excessive moisture increases the risk of drowning (Beirne 1970, Burton et al. 1980). Under favorable conditions, larvae complete development and construct a pupal cell, which can only be formed in either solid or wet soil, bound together via salivary secretions (Strickland 1916, Burton et al. 1980). Although wet soil conditions often facilitate pupation, excess moisture can also promote fungal growth, forcing larvae to the soil surface where they are vulnerable to additional threats such as parasites, predators, and disease (Walkden 1950, Beirne 1970, Hardwick and Lefkovitch 1971).

Larvae that survive external stressors such as desiccation, flooding, predation, and disease emerge as adults in late spring to early summer, depending on latitude (Burton et al. 1980, Kendall et al. 1981). Upon emergence, adults enter a migratory phase, flying to the Rocky Mountains (Pruess and Pruess 1971, Kendall et al. 1981, Dittemore et al. 2023). Once in alpine environments, moths feed nocturnally on the nectar of alpine flowers, accumulating lipid stores necessary for both reproduction and the return migration to natal ranges in late summer and early fall (Kendall et al. 1981, White et al. 1998b). These lipids aid in sexual maturation, ensuring that upon their return, females are physiologically prepared to oviposit, thus continuing the life cycle (Kendall et al. 1981, White et al. 1998b).

Low elevation ecology

Agricultural significance

Euxoa auxiliaris has been recognized as an agricultural pest since the late 1800s due to its ability to damage a wide variety of cereal and forage crops across agricultural landscapes (Walkden 1950, Burton et al. 1980). Although it is considered a polyphagous species, larvae exhibit feeding preferences for dandelion, winter wheat, winter barley, and alfalfa, which serve as primary hosts during development (Walkden 1950, Pruess 1961, Manglitz et al. 1973). Under favorable conditions, populations can reach outbreak levels, with densities as high as 45 larvae/m^2, leading to substantial crop losses (Strickland 1916, Walkden 1950, Ellis 2014). When food sources become scarce, larvae will resort to cannibalism, further influencing population dynamics (Strickland 1916).

Outbreaks are typically infrequent, often following one or two years of low population densities before reaching economically damaging levels (Beirne 1970). However, historical records suggest this pattern is not consistent. During the 1950s, annual infestations were documented across Montana, Wyoming, Colorado, Alberta, and Saskatchewan, demonstrating the broad geographic range and the potential for sustained economic impact (Jacobson and Blakeley 1959). Similarly, Nebraska experienced consecutive outbreaks from 1968 to 1970, prompting researchers to assess the effectiveness of various insecticides for controlling infestations (Manglitz et al. 1973). The economic consequences of these outbreaks can be substantial; in 1990 alone, army cutworm outbreaks affected more than 10,000 ha in southern

Alberta, with more than 6,000 ha requiring insecticide treatment to mitigate crop losses (Jones et al. 1990).

The widespread use of insecticides to control army cutworm populations has raised concerns about the potential for pesticide bioaccumulation in these moths and subsequent exposure risk to higher trophic levels. Grizzly bears, which rely on *E. auxiliaris* aggregations as a key seasonal food source in alpine environments, may be particularly vulnerable to pesticide transfer through the food chain (French et al. 1994, White et al. 1999, Robison et al. 2006). However, analysis of moth samples collected from alpine feeding sites in the Absaroka Mountain Range revealed only trace levels of pesticide residues, concentrations deemed too low to pose a physiological risk based on estimated moth consumption rates by bears (Robison 2009).

High elevation ecology

Migration

Euxoa auxiliaris was originally thought to be a bivoltine species, a hypothesis used to explain its sudden disappearance from the Great Plains during summer months (Gillette 1903). However, subsequent research suggested that rather than undergoing a second generation, the moths instead aestivated near their emergence sites. This explanation was challenged by Pepper (1932), who found that moths were unable to survive the summer months in field cages but could be maintained at lower temperatures in cold cabinets. These findings led to the proposal that *E. auxiliaris* undertake a unidirectional flight to higher elevations, where they could successfully aestivate in cooler conditions (Pepper 1932). The presence of *E. auxiliaris* in high-altitude regions of Montana and Colorado refined this hypothesis, suggesting that instead of prolonged aestivation, the moths exhibit diurnal quiescence (Chapman et al. 1955, Kendall et al. 1981).

Evidence supporting the connection between these high-altitude populations and those in the Great Plains came from experimental observations revealing the moths' capacity for long-distance flight, after consuming nectar, indicating the migratory potential for this species (Koerwitz and Pruess 1964). This experimental evidence of sustained flight was later supported by field observations in Nebraska, where black light trap collections documented a seasonal movement pattern (Pruess 1967, Pruess and Pruess 1971). Moths were captured during May and June, then again in September and October, suggesting a predictable migratory cycle (Pruess 1967). The spring migration was directionally oriented east to west and occurred at wind-assisted altitudes (Pruess and Pruess 1971).

Wind-assisted flight is a well-documented strategy among migratory noctuids. For instance, the black cutworm (*Agrotis ipsilon*) uses synoptic weather patterns to aid in long-distance transport, with migratory events successfully predicted using meteorological models (Showers et al. 1989). Similarly, wind is a major factor in the migratory expansion of the fall armyworm (*Spodoptera frugiperda*), which recently established populations in Australia, a movement reconstructed using trajectory modeling (Qi et al. 2021). These migrations typically occur below 1,500 m, placing them within the low-level jet stream, a key driver for long-range transport (Showers et al. 1989). The low-level jet occurs in the atmospheric boundary layer common in the Great Plains, forming around dusk and peaking in intensity around midnight, with strong winds predominantly moving southward (Arritt et al. 1997, Walters et al. 2008). Given these parallels, *E. auxiliaris* may also capitalize on this jet stream to assist with their seasonal movements between natal ranges and alpine habitats.

However, noctuid migration is not solely dictated by passive wind transport. When wind patterns deviate from their intended route, noctuids actively adjust their heading to compensate for displacement (Chapman et al. 2008, Chapman et al. 2011b). This ability to maintain a directed course suggests an underlying navigational mechanism, referred to as a compass-biased downstream orientation, likely guided by visual cues and Earth's magnetic field (Chapman et al. 2008, Chapman et al. 2011b, Merlin et al. 2012). If *E. auxiliaris* employs a similar strategy, it may exercise some degree of control over its migration destination, rather than relying entirely on favorable wind currents.

Despite the advantages of wind-assisted migration, *E. auxiliaris* faces physiological and environmental constraints that can influence its movement patterns. Energy reserves and abiotic conditions are primary influencers in determining the success of its annual westward migration (Koerwitz and Pruess 1964). Moths rely on favorable weather fronts to aid their journey, stopping periodically to refuel on nectar (O'Brien and Lindzey 1994, Kevan and Kendall 1997, White et al. 1998b). Although lipid reserves from the pupal stage provide an initial energy source, these are insufficient for sustained flight, necessitating continuous replenishment along the journey (Koerwitz and Pruess 1964). Similarly, the return migration to natal ranges is supported by seasonal increases in whole-body lipid content, but even with these additional reserves, energy availability alone is insufficient to meet migratory distance requirements, suggesting the use of tailwinds to circumvent these limitations and reduce transportation costs (White et al. 1998b).

The increase in seasonal whole-lipid content that aids in the return migration occurs in the alpine habitat. Nocturnal feeding facilitates this fat accumulation, allowing moths to store energy reserves that can reach up to 85% of body weight by late summer—a substantial increase from the 20–34% observed in newly emerged adults (Kevan and Kendall 1997, White et al. 1998b, White et al. 1999). These stored lipids not only fuel the return migration but also support sexual maturation (Pruess 1963, French et al. 1994, Kevan and Kendall 1997). *Euxoa auxiliaris* exhibits oogenesis flight syndrome, a strategy in which reproductive development is temporarily suppressed to prioritize migratory potential (Koerwitz and Pruess 1964, Pruess 1967, Rankin et al. 1986, Kevan and Kendall 1997). The seasonal increase in lipid content facilitates reproduction (Pruess 1963, French et al. 1994). As moths journey back to natal ranges, mating and egg maturation occur primarily between the Rocky Mountains and final destination, ensuring that oviposition takes place upon arrival (Pruess 1967, White et al. 1998b).

Methods for tracking

Radar

The application of radar in entomology began in the 1950s with the detection of desert locust (*Schistocerca gregaria*) migration in the Persian Gulf (Rainey 1967). Since then, the technology has developed into an effective tool for measuring and characterizing features of insect migration that cannot be obtained from traditional methods like light-trap catches or other ground-based observations, which are often affected by weather conditions and logistical challenges (Chapman et al. 2003). One of radar's key advantages is its ability to remotely quantify insect biomass and assess aspects of migratory behavior, such as displacement and orientation (Chapman et al. 2003). Early studies relied on X-band scanning radar, which tracked the spatial and temporal distribution of migratory insects (Chapman et al. 2003). The integration of radar with meteorological data further refined these analyses, revealing how insects exploit synoptic weather patterns to optimize migration. For example, Beerwinkle et al. (1994) demonstrated that nocturnal low-level wind jets facilitate long-distance insect movement.

The U.S. national network of WSR-88D Doppler radars, although originally developed for weather monitoring, are like X-band radars in that they use scanning technology to track airborne targets (Westbrook 2008). However, their increased power allows for higher-altitude detection compared to X-band radars, and in turn, better calculation of the flight speed and heading of migrating noctuids, offering monitoring capabilities at large spatial scales (Westbrook 2008).

Advancements in target identity led to the development of harmonic and vertical-looking radar (VLR) in the early 1990s (Chapman et al. 2011a). Harmonic radar, which relies on echoes from a tag placed on an individual insect transmitted within a range of 900 m is not suitable for studying mass movements. Therefore, VLR and X-band radar have been the primary tools for investigating noctuid migration (Westbrook 2008, Chapman et al. 2011a). VLR, specifically, provided a major advancement in monitoring capabilities, enabling more accurate and detailed studies of insect movement (Chapman et al. 2003). The VLR system rotates the radar beam's plane of polarization which allows data collection on radar reflectivity, body alignment, wingbeat frequency, insect body mass, and shape to be deduced, which is critical information for identifying target species and assessing orientation behavior (Chapman et al. 2003). However, the mechanism and adaptive significance of these characteristics to migratory behavior remains speculative (Wood et al. 2006).

For example, studies on the silver Y moth (*Autographa gamma*), a noctuid that migrates between Northern Europe and Africa, revealed a compass-based mechanism for flight-altitude optimization and cross-wind drift compensation (Chapman et al. 2008). These navigational cues are believed to be either geomagnetic or visual in nature and may be influencing movement patterns (Chapman et al. 2008, Dreyer et al. 2018).

Recent research has applied radar technology to *E. auxiliaris* migration, improving our understanding of their seasonal movements. Dittemore (2022) investigated *E. auxiliaris* migration in the GYE using X-band radar to estimate biomass and heading of noctuids during the known spring migration period. The results revealed a correlation between flight direction and location of known summer alpine moth aggregation sites (Dittemore 2022). Target identification and biomass estimates were refined using supplemental data on wingbeat frequency and density during peak flight times (Dittemore 2022). Although this research provided valuable insights into *E. auxiliaris* migration in alpine environments, further study is needed to better understand the drivers and variability of these movements.

Other insect-tracking methods

Tracking insect migration presents unique challenges, requiring at times innovative approaches to infer movement across great distances. Pollen analysis has proven to be a valuable tool in this effort, offering supporting evidence of long-range dispersal. For example, the presence of exotic pollen on the proboscis of corn earworm (*Helicoverpa zea* (Boddie)) provided insight into its movement from southern Texas to Arkansas (Hendrix et al. 1987). A similar approach confirmed the migratory pathways of the black cutworm (*Agrotis ipsilon*) and *M. unipuncta* from Texas to Missouri (Hendrix and Showers 1992). Given its success in tracking other noctuid species, pollen analysis has been suggested as a method for identifying the natal origin of *E. auxiliaris*, but it has yet to be applied to this species (O'Brian and Lindzey 1994).

Beyond pollen analysis, genetic tools have provided further insights into insect movement. Microsatellite analysis of *E. auxiliaris* collected from both lowland and alpine sites revealed a panmictic population structure, suggesting high gene flow and broad distribution across the Rocky Mountains (Robison 2009). These findings underscore the species' extensive movement capabilities across different elevations, reinforcing the need for additional methods to refine our understanding of migration routes.

More recently, stable isotope analysis has emerged as a valuable tool for studying large-scale insect movements. The stable hydrogen isotope composition of the metabolically inert tissues of insect wings preserves the isotopic signature of larval food sources, allowing researchers to infer natal origins (Hobson et al. 2018). Dittemore et al. (2023) applied this approach to *E. auxiliaris*, providing the first direct evidence of north-to-south migration, with natal origins extending into Canada. This study marks a remarkable step forward in understanding the species' migratory patterns and highlights the potential for isotopic analysis to complement other tracking methods in future research.

Temperature

Euxoa auxiliaris occupies a diverse range of climatic conditions, yet the effects of temperature on their migration, reproduction, fitness, and geographic distribution have been poorly understood. Given that temperature plays a fundamental role in insect physiology, shaping metabolic efficiency, development, and movement (Shah et al. 2021), it is likely a key factor in the species' migratory ecology. Studies on another migratory noctuid, the native budworm (*Helicoverpa punctigera*), have shown that rising temperatures reduce metabolic efficiency, leading to changes in growth and dispersal patterns (Bawa et al. 2021). These findings suggest that *E. auxiliaris* may experience similar temperature-driven constraints on its movement and life history.

As early as 1931, temperature was hypothesized as a motivating factor in the westward migration of *E. auxiliaris* when it was observed that individuals were unable to survive the extreme summer heat of the Great Plains (Pepper 1932). Seeking more favorable conditions, migrating moths reach alpine environments where they encounter substantial temperature gradients, with surface rocks reaching ~40 °C while soil temperatures in talus fields can drop below freezing (French et al. 1994). These fluctuations can not only impact moth behavior and survival but also influence their susceptibility to predation. At cooler temperatures, moths exhibit slowed movement, reducing their ability to evade excavation by grizzly bears, which can impact feeding success (Mattson et al. 1991b, French et al. 1994).

Because temperature directly affects metabolic rate, it has major implications for energy storage and use in insects (Arrese and Soulages 2010). *Euxoa auxiliaris* rely on alpine nectar sources to build abdominal lipid reserves, which fuel sexual maturation and the return migration (Pruess 1967, Kevan and Kendall 1997). Their apparent heat aversion and cold tolerance as adults suggest that both upper and lower thermal limits warrant further investigation. A deeper understanding of these tolerances could provide critical insight into habitat selection, distribution patterns, and the availability of late-season food sources for grizzly bears.

Characteristics of Alpine Moth Aggregation Sites

Upon reaching the alpine elevations of the Rocky Mountains, *E. auxiliaris* aggregate in talus and boulder fields, selecting sites that share key environmental characteristics such as elevation, aspect, slope, geomorphological features, and the presence of water (French et al.

1994, White et al. 1998a, O'Brien and Lindzey 1998). Although these factors vary regionally with climate, water availability remains a consistent feature across aggregation sites, primarily sourced from glacial or snowmelt (French et al. 1994, O'Brien and Lindzey 1998). This water is not only essential for avoidance of desiccation in an otherwise dry environment, but also for sustaining vegetative growth in nearby meadows and tundra (French et al. 1994, White et al. 1998a).

Although moth aggregation sites themselves are largely barren, their proximity to alpine meadows and tundra provides access to floral nectar resources necessary for sustaining moths (Kendall et al. 1981, White et al. 1998a, Lozano 2022). However, regional variation in plant communities may influence foraging behavior. For instance, in the St. Jemez mountains of New Mexico, aggregation sites are surrounded by coniferous forests and grasslands rather than alpine meadows, suggesting moths in this region have to forage farther from aggregation sites to meet energy requirements (Coop et al. 2005). Despite the importance of floral resources, a comprehensive list of adult food sources has yet to be established. Observations from alpine sites in Nevada, Colorado, Montana, and Wyoming confirm active feeding with *E. auxiliaris* having been documented visiting flowers such as *Mertensia lanceolata*, *Senecio crassulus*, *Pedicularis groenlandica*, *Valeriana capitata*, *Bistorta bistortoides*, and *Haplopappus lyallii* in various habitats (Chapman et al. 1955, Kendall et al. 1981, French et al. 1994).

Aggregation sites are typically found in association with snowfields, glacial cirques, and hanging valleys, forming on bare talus slopes immediately beneath parent rock (Mattson et al. 1991b, French et al. 1994, O'Brien and Lindzey 1998). In the GYE, talus fields must possess specific thermal and structural characteristics to support moth aggregation. Although some sites may appear suitable based on surface features, Robison (2009) observed that moths were absent from areas where the talus was too shallow, likely due to an insufficient thermal gradient needed for thermoregulation.

These thermal gradients fluctuate substantially, with rock surface temperatures ranging from -2 to 25 °C, and occasionally exceeding 40 °C, while temperatures 20–30 cm below the rock surface can remain below freezing (French et al. 1994, White et al. 1998a). This sharp contrast in temperature likely plays a role in moth distribution within the talus, as individuals seek microhabitats that allow them to regulate body temperature while avoiding extreme conditions (French et al. 1994, White et al. 1998b).

During the day, *E. auxiliaris* primarily remain deep within the talus, a behavior thought to reduce exposure to predators and harsh weather. This refuge is especially beneficial when grizzly bears excavate the rocks in search of moths, as individuals can retreat further into the talus to evade predation (French et al. 1994). However, those quickly turned over from the cool talus to the rock surface often struggle to warm up their flight muscles quickly enough for escape, increasing their susceptibility to predation by bears (French et al. 1994).

Even though microhabitats within the talus provide thermal refuges for *E. auxiliaris*, broader environmental factors such as elevation and aspect also shape the distribution of aggregation sites. Site elevations can vary widely across mountain ranges, ranging from 1,830 m in the Absaroka range to 4,197 m in the Tetons, with most aggregation sites occurring between 2,700–3,500 m (Mattson et al. 1991b, French et al. 1994, White et al. 1998a, Robison et al. 2006). These sites have been located on all aspects, but studies have consistently documented a preference for southern to western aspects (Mattson et al. 1991b, O'Brien and Lindzey 1998, White et al. 1998a). This was particularly true in Glacier National Park (GNP) with all known aggregation sites located on southern or western aspects (White et al. 1998a). Similarly, in the GYE, O'Brien and Lindzey (1998) found sites most commonly situated on southern aspects with none occurring on northern-facing slopes. This pattern contrasts with findings by Coop et al. (2005) in the Jemez mountains of New Mexico, where moth aggregation sites were located on predominantly northern aspects. Such regional differences may best be explained by Kendall et al. (1981), who noted study site selection is often constrained by accessibility and safety, potentially influencing reported distributions.

Temporal abundance and measuring moth abundance at alpine sites.

In the northern Rocky Mountains, *E. auxiliaris* typically arrives between late June and early July, coinciding with snowmelt and the onset of the alpine flowering season (French et al. 1994). Throughout the summer, these moths generally exhibit an upslope movement, likely in response to shifting nectar availability. However, when movements occur downslope, lower seasonal temperatures and higher moisture conditions have been recorded at these lower elevations (Pruess 1967, Kevan and Kendall 1997). Kendall et al. (1981) also documented what appeared to be a downslope movement later in the season, suggesting it could be a late-stage upward migration or, more likely, the return migration to their natal ranges as nectar sources dwindle. In the GYE and farther south, their return migration occurs between early September to October as confirmed by blacklight trapping studies (Pruess 1967, O'Brien and Lindzey 1994, Kevan and Kendall 1997).

The timing of moth migration is relatively well established, however, estimating their distribution at aggregation sites remains challenging. Excavations by bears provide indirect evidence of moth presence, occurring in talus fields with rocks 10–60 cm in diameter and typically 15–50 cm deep. However, accurately estimating moth density is difficult, as bears backfill excavations as they move through the terrain (Mattson et al. 1991b). In the GNP and GYE, bear scat analysis has been used to estimate moth abundance at aggregation sites (White et al. 1999, Gunther et al. 2014, Nunlist 2020, Lozano 2022). For instance, Nunlist (2020) found 67% of bear activity was attributed to moth foraging, with scat analysis revealing that approximately 20% of sample volume consisted of *E. auxiliaris.* These findings were corroborated by Lozano (2022), who later documented a single scat sample containing approximately 6,000 moths. However, these estimates may not fully represent the actual moth population in talus fields due to variations in bear foraging behavior and the availability of scats for analysis (White et al. 1998a). Hand excavations have also been conducted in the field, but the moths' ability to escape, either by flying away or retreating into talus, complicates efforts to assess abundance (French et al. 1994). Dittemore et al. (2023) had success with hand-collection of *E. auxiliaris* in high-elevational talus in the Absaroka Range, although these data were not used in abundance studies.

Collecting data on moth distributions is further complicated by environmental and methodological constraints. Field studies are often hindered by the remote and rugged terrain of high-elevation talus fields, making site accessibility a serious limitation. Researchers must also balance data collection efforts with minimizing disturbance to foraging bears, as unnecessary displacement could alter natural foraging behaviors and impact study results. Additionally, safety concerns including the risk of encountering bears in proximity further restrict fieldwork, requiring careful planning and adherence to safety protocols (White et al. 1999)

Beyond these environmental and safety-related obstacles, logistical challenges add another layer of difficulty. Transporting and deploying essential equipment such as blacklights, insect traps, and storage containers can be cumbersome, especially in steep and rocky landscapes where maneuverability is restricted. The weight and bulk of this equipment often limit the number of sampling sites that can be accessed within a given timeframe. Considering these constraints, sampling efforts must be both extensive and strategically distributed to generate representative population density estimates, which are essential for understanding long-term population trends and the ecological importance of *E. auxiliaris* in alpine ecosystems.

Research objectives

Euxoa auxiliaris have only been recognized as an important food source for grizzly bears in the GYE since the 1980s (Mattson et al. 1991b). Despite their ecological importance, many aspects of their population dynamics and the environmental drivers influencing moth abundance remain poorly understood. In particular, there is limited knowledge of *E. auxiliaris* migratory patterns and the influence of abiotic factors on flight behavior. Additionally, given the various constraints with direct study of moth abundance in alpine sites, alternative methods for quantifying numbers and calorie flux of *E. auxiliaris* in the GYE are essential, especially given the role these moths play in grizzly bear foraging ecology. Expanding our knowledge of the bear and moth relationship will help inform grizzly bear management plans in the GYE and assess the long-term stability of this important food source for a protected species.

Therefore, my study had two objectives: (1) estimate *E. auxiliaris* numbers and calorie flux in the GYE using radar along the eastern front range of the Absaroka Mountain range; and (2) determine the environmental and biological factors that may influence migratory flight behavior and dynamics. Objective 2 was addressed in two parts: (1) identify the critical thermal minimum and maximum of *E. auxiliaris*; and (2) determine the wingbeat frequency of *E. auxiliaris* under the influence of different environmental factors.

References

Arrese EL, Soulages JL. 2010. Insect fat body: energy, metabolism, and regulation. *Annual Review of Entomology*. *55*(1): 207–225. https://doi.org/10.1146/annurev-ento-112408-085356

Arritt RW, Rink TD, Segal M, et al. 1997. The Great Plains low-level jet during the warm season of 1993. *Monthly Weather Review*. *125*(9): 2176–2192. https://doi.org/10.1175/1520 0493(1997)125%3C2176:TGPLLJ%3E2.0.CO;2

Beirne BP. 1970. Effects of precipitation on crop insects. *The Canadian Entomologist. 102*(11): 1360–1373. https://doi.org/10.4039/Ent1021360-11

Bawa SA, Gregg PC, Soccoro APD, et al. 2021. Estimating the differences in critical thermal maximum and metabolic rate of *Helicoverpa punctigera* (Wallengren) (Lepidoptera: Noctuidae) across life stages. *PeerJ*. *9*:e12479. https://doi.org/10.7717/peerj.12479

Beerwinkle KR, Lopez JD, JR, et al. 1994. Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. *Environmental Entomology. 23*(3): 676–683. https://doi.org/10.1093/ee/23.3.676

Burton. RL, Starks KJ, Peters DC. 1980. The army cutworm. *Bulletin-Agricultural Experiment Station, Oklahoma State University*. *Bulletin. 749*: 35. https://openresearch.okstate.edu/server/api/core/bitstreams/cbe80810-362e-4c61-b926-9dc2929ea56e/content

Chapman JA, Romer JI, Stark J. 1955. Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology*. *36*(1): 156–158. https://doi.org/10.2307/1931444

Chapman JW, Drake VA, Reynolds DR. 2011a. Recent insights from radar studies of insect flight. *Annual Review of Entomology*. *56*(1): 337–356. https://doi.org/10.1146/annurev-ento-120709-144820

Chapman JW, Reynolds DR, Smith AD. 2003. Vertical-looking radar: a new tool for monitoring high-altitude insect migration. *BioScience, 53*(5): 503–511. https://doi.org/10.1641/0006-3568(2003)053[0503:Vrantf]2.0.Co;2

Chapman JW, Reynolds DR, Hill JK, et al. 2008. A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology. 18*(19): R908–R909. https://doi.org/10.1016/j.cub.2008.08.014

Chapman JW, Klaassen RH, Drake VA, et al. 2011b. Animal orientation strategies for movement in flows. *Current Biology*. *21*(20): R861–R870. https://doi.org/10.1016/j.cub.2011.08.014

Cooley RA. 1916. Observations on the life history of the army cutworm, *Chorizagrotis auxiliaris*. *Journal of Agricultural Research. 6*(23): 871–881. https://www.cabidigitallibrary.org/doi/full/10.5555/19160500950

Coop JD, Hibner CD, Miller AJ, et al. 2005. Black bears forage on army cutworm moth aggregations in the Jemez Mountains, New Mexico. *The Southwestern Naturalist. 50*(2): 278–281. https://doi.org/10.1894/0038-4909(2005)050[0278:BBFOAC]2.0.CO;2

Dittemore CM. 2022. Natal Origin, Migratory Patterns, and Abundance of the Army Cutworm, *Euxoa auxiliaris.* Thesis. Montana State University, Bozeman, Montana. https://scholarworks.montana.edu/items/e08ebc9c-351c-4a11-889a-341e45c88820?show=full

Dittemore CM, Tyers DB, Weaver DK, et al. 2023. Using stable isotopes to determine natal origin and feeding habits of the army cutworm moth, *Euxoa auxiliaris,* (Lepidoptera: Noctuidae). *Environmental Entomology*. *52*(2): 230–242. https://doi.org/10.1093/ee/nvad006

Drecktrah HG. 1978. Morphology of the internal reproductive system of the adult female army cutworm, *Euxoa auxiliaris*. *Annals of the Entomological Society of America*. *71*(6): 923–927. https://doi.org/10.1093/aesa/71.6.923

Dreyer D, Frost B, Mouritsen H, et al. 2018. The earth's magnetic field and visual landmarks steer migratory flight behavior in the nocturnal Australian bogong moth. *Current Biology*. *28*(13): 2160–2166.e5. https://doi.org/10.1016/j.cub.2018.05.030

Ellis S. 2014. Cutworms damage fields in Oregon, Idaho, *Sugar Producer Magazine*. April 30, 2014. https://www.sugarproducer.com/2014/04/cutworms-damage-fields-in-oregon

Floate KD, Hervet VA. 2017. Noctuid (Lepidoptera: Noctuidae) pests of canola in North America. In *Integrated management of insect pests on canola and other Brassica oilseed crops.* p. 96–113. Wallingford UK: CABI. http://ebookcentral.proquest.com/lib/montana/detail.action?docID=5898008

French SP, French MG, Knight RR. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *Bears: Their Biology and Management. 9*: 389–399. https://doi.org/10.2307/3872725

Gillette CP. 1903. Some of the more important insects of 1903. *Bulletin of the Colorado Agriculture Experiment Station*. *94*. https://books.google.com/books?hl=en&lr=&id=y4QoAAAAYAAJ&oi=fnd&pg=PA3&dq=Gillette,+C.+P.+1903.+Some+of+the+more+important+insects+of+1903.+Bulletin+of+the+Colorado+Agriculture+Experiment+Station,+94.+&ots=F5tcyjfXbW&sig=iqIemFZRAIDpFWt_MwKehmw-Jrw#v=onepage&q&f=false

Gunther KA, Shoemaker RR, Frey KL, et al. 2014. Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus*. *25*(1): 60–72. https://doi.org/10.2192/URSUS-D-13-00008.1

Hardwick DF, Lefkovitch P. 1971. Physical and biotic factors affecting *Euxoa* species abundance in western North America: A regression analysis. *The Canadian Entomologist*. *103*(9): 1217–1235. https://doi.org/10.4039/Ent1031217-9

Hendrix III W, Mueller T, Phillips J, et al. 1987. Pollen as an indicator of long-distance movement of *Heliothis zea* (Lepidoptera: Noctuidae). *Environmental Entomology. 16*(5): 1148–1151. https://doi.org/10.1093/ee/16.5.1148

Hendrix WH, Showers WB. 1992. Tracing black cutworm and armyworm (Lepidoptera: Noctuidae) northward migration using *Pithecellobium* and *Calliandra* pollen. *Environmental Entomology*. *21*(5): 1092–1096. https://doi.org/10.1093/ee/21.5.1092

Hobson KA, Doward K, Kardynal KJ, Mcneil JN. 2018. Inferring origins of migrating insects using isoscapes: A case study using the true armyworm, *Mythimna unipunct*a, in North America. *Ecological Entomology*. *43*(3): 332–341. https://doi.org/10.1111/een.12505

Jacobson LA, Blakeley PE. 1959. Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America. 52*(1): 100–105. https://doi.org/10.1093/aesa/52.1.100

Jones HW, Byers JR, Butts RA, et al. 1990. Insects and related pests of cereal crops –Alberta. *The Canadian Agricultural Insect Pest Review.* 68: 13–14.

Kendall DM, Kevan PG, LaFontaine JD. 1981. Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist. 113*(7): 607–614. https://doi.org/10.4039/Ent113607-7

Keosentse O, Mutamiswa R, Du Plessis H, et al. 2021. Developmental stage variation in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) low temperature tolerance: implications for overwintering. *Austral Entomology*. *60*(2): 400–410. https://doi.org/10.1111/aen.12536

Kevan PG, Kendall DM. 1997. Liquid assets for fat bankers: Summer nectarivory by migratory moths in the Rocky Mountains, Colorado, U.S.A. *Arctic and Alpine Research. 29*(4): 478–482. https://www.tandfonline.com/doi/abs/10.1080/00040851.1997.12003268

Koerwitz F, Pruess K. 1964. Migratory potential of the army cutworm. *Journal of the Kansas Entomological Society. 37*(3): 234–239. https://www.jstor.org/stable/25083389

Lozano KN. 2022. Food Resources for Grizzly Bears at Army Cutworm Moth Aggregation Sites in the Greater Yellowstone Ecosystem. Thesis. Montana State University, Bozeman, Montana. https://scholarworks.montana.edu/items/7e29c334-2f1e-4dc3-a569-112298192290

Manglitz GR, Schalk JM, Andersen LW, et al. 1973. Control of the army cutworm on alfalfa in Nebraska. *Journal of Economic Entomology*. *66*(1): 299–299. https://doi.org/10.1093/jee/66.1.299

Mattson DJ, Gillin CM, Benson SA, et al. 1991b. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology*. *69*(9): 2430–2435. https://doi.org/10.1139/z91-341

Merlin C, Heinze S, Reppert SM. 2012. Unraveling navigational strategies in migratory insects. *Current opinion in neurobiology*. *22*(2): 353–361. https://doi.org/10.1016/j.conb.2011.11.009

Michaud JP, Martin TJ, Jyoti JL. 2006. Larval preference for a wheat cultivar in the army cutworm (Lepidoptera: Noctuidae). *Journal of the Kansas Entomological Society*. *79*(1): 28–33. https://doi.org/10.2317/0022-8567(2006)079[0028:LPFAWC]2.0.CO;2

Nunlist E. A. 2020. Grizzly bears and humans at two moth aggregation sites in Wyoming. Thesis. Montana State University. Bozeman, Montana. https://scholarworks.montana.edu/items/a931b40e-9183-4075-8000-17409fae0376

O'Brien SL, Lindzey F. 1994. Grizzly bear use of moth aggregation sites and summer ecology of army cutworm moths in the Absaroka Mountains, Wyoming. *Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming.* https://search.worldcat.org/it/title/Grizzly-bear-use-of-moth-aggregation-sites-and-summer-ecology-of-army-cutworm-moths-in-the-Absaroka-Mountains-Wyoming-:-final-report/oclc/48960914

O'Brien SL, Lindzey FG. 1998. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*. p. 427–435. https://www.jstor.org/stable/3873154

Pepper J. 1932. Observations on a unidirectional flight of army cutworm moths and their possible bearing on aestivation. *The Canadian Entomologist.* *64*(11): 241–242. https://doi.org/10.4039/Ent64241-11

Pruess KP. 1961. Distribution of army cutworm larvae in wheat and barley fields. *Journal of Economic Entomology*. *54*(2): 250–252. https://doi.org/10.1093/jee/54.2.250

Pruess, K. P. 1963. Effects of food, temperature, and oviposition site on longevity and fecundity of the army cutworm*, Chorizagrotis Auxiliaris. Journal of Economic Entomology. 56*(2), 219–221. https://academic.oup.com/jee/article/56/2/219/2207489

Pruess KP. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaries* (Lepidoptera: Noctuidae). I. Evidence for a migration. *Annals of the Entomological Society of America. 60*(5): 910–920. https://doi.org/10.1093/aesa/60.5.910

Pruess KP, Pruess NC. 1971. Telescopic observation of the moon as a means for observing migration of the army cutworm, *Chorizagrotis Auxiliaris* (Lepidoptera: Noctuidae). *Ecology*. *52*(6): 999–1007. https://doi.org/10.2307/1933805

Qi G-J, Ma J, Wan J, et al. 2021. Source regions of the first immigration of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) invading Australia. *Insects*. *12*(12) https://doi.org/10.3390/insects12121104

Rainey RC. 1967. Radar observations of locust swarms. *Science*. *157*(3784): 98–99. https://doi.org/10.1126/science.157.3784.98

Rankin MA, McAnelly ML, Bodenhamer JE. 1986. The oogenesis-flight syndrome revisited. In *Insect flight: dispersal and migration*. p. 27–48. Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-71155-8_3

Robison HL. 2009. Relationships between Army Cutworm Moths and Grizzly Bear Conservation. Thesis. University of Nevada, Reno, Nevada. https://scholarwolf.unr.edu/items/e79fffbe-49b1-4762-be75-bb2194008c0b

Robison HL, Schwartz CC, Petty JD, et al. 2006. Assessment of pesticide residues in army cutworm moths (*Euxoa auxiliaris*) from the Greater Yellowstone Ecosystem and their potential consequences to foraging grizzly bears (*Ursus arctos horribilis*). *Chemosphere. 64*(10): 1704–1712. https://doi.org/10.1016/j.chemosphere.2006.01.006

Shah AA, Woods HA, Havird JC, et al. 2021. Temperature dependence of metabolic rate in tropical and temperate aquatic insects: Support for the climate variability hypothesis in mayflies but not stoneflies. *Global Change Biology*. *27*(2): 297–311. https://doi.org/10.1111/gcb.15400

Showers WB, Whitford F, Smelser RB, et al. 1989. Direct evidence for meteorologically driven long-range dispersal of an economically important moth. *Ecology. 70*: 987–992. https://doi.org/10.2307/1941366

Snow SJ. 1925. Observations on the cutworm, *Euxoa auxiliaris* Grote, and its principal parasites. *Journal of Economic Entomology. 18*(4): 602–609. https://doi.org/10.1093/jee/18.4.602

Strickland EH. 1916. The army cutworm: *Euxoa* (*Chorizagrotis*) *auxiliaris* Grote. *Canadian Department of Agricultural Entomology*. (Bulletin No. 13). https://www.canadiana.ca/view/oocihm.83630/1

Walkden HH. 1950. Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains. *U.S. Dept. of Agriculture*. p. 1–58. https://www.biodiversitylibrary.org/item/130872

Walters CK, Winkler JA, Shadbolt RP, et al. 2008. A long-term climatology of southerly and northerly low-level jets for the Central United States. *Annals of the Association of American Geographers*. *98*(3): 521–552. https://doi.org/10.1080/00045600802046387

Westbrook JK. 2008. Noctuid migration in Texas within the nocturnal aeroecological boundary layer. *Integrative and Comparative Biology*. *48*(1): 99–106. https://doi.org/10.1093/icb/icn040

White Jr D, Kendall KC, Picton HD. 1998a. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology*. *76*(2): 221–227. https://doi.org/10.1139/z97-185

White Jr D, Kendall KC, Picton HD. 1998b. Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology. 76*(5): 835–842. https://doi.org/10.1139/z98-001

White Jr D, Kendall KC, Picton HD. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildlife Society Bulletin*. p. 146–151. https://www.jstor.org/stable/3783951

Wilcox EV. 1898. The grain aphis. An army cut-worm. *Montana Agricultural Experiment Station*, (Bulletin No. 17). https://catalog.hathitrust.org/Record/011481195

Wood CR, Chapman JW, Reynolds DR, et al. 2006. The influence of the atmospheric boundary layer on nocturnal layers of noctuids and other moths migrating over southern Britain. *International Journal of Biometeorology*. *50*(4): 193–204. https://doi.org/10.1007/s00484-005-0014-7

CHAPTER TWO

CRITICAL THERMAL LIMITS OF THE SEASONAL MIGRANT, *EUXOA AUXILIARIS* (LEPIDOPTERA: NOCTUIDAE)

Abstract

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.

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 ($\mathrm{CTL}_{\mathrm{max}}$) and lower ($\mathrm{CTL}_{\mathrm{min}}$) 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. 1998b). 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. 1991b, 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-caught *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 higher-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 20–30 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 22–27 °C and 50–60% relative humidity (RH) until hatch (Jacobson and Blakely 1959).

Second generation larvae were used for CTL assays. Larvae were reared at 22–27 °C and 50–60% 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 days based on frequency of feeding and condition of diet. Pupation occurred inside the diet cups. Pupae were left undisturbed for 3–4 days within the cups to minimize the risk of damaging the newly formed pupae. After 3–4 days, pupae were transferred from individual diet cups onto paper towel-lined, ventilated 5.7-L plastic containers.

Approximately 25–35 pupae were placed in each container. Pupae were retained in total darkness at ambient temperatures of 22–27 °C and 50–60% 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 1–5 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 22–27 °C and 50–60% RH until experimental testing. Each cage contained 20–30 moths; and paper towels were provided for cover. Moths were fed a 10% sugar solution provided on a soaked cotton ball, which were replaced daily. Wild-caught moths were used for experimental testing within 1–12 days 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 x 26.7 cm x 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).

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 6 trials were conducted using lab-reared moths, age 1–11 days post emergence, and a total of 8 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–

16 days 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 were conducted using the *cor.test* function in base R, and 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 one-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.

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 43.72–44.56 °C (Fig. 3). The average CTL_{max} for wild-caught moths across 8 trials was 43.28 °C with a range of 42.04–44.26 °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 $\mathrm{CTL}_{\mathrm{max}}$ moths (0.1519 g). The average wet weight of lab-reared $\mathrm{CTL}_{\mathrm{min}}$ 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 $\mathrm{CTL}_{\mathrm{min}}$ 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 $\mathrm{CTL}_{\mathrm{min}}$ (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 $\mathrm{CTL}_{\mathrm{min}}$ ($R^2 = 0.1139$, adjusted $R^2 = 0.0933$, $F = 5.528$, df = 43, $P = 0.0234$). However, the relationship between $\mathrm{CTL}_{\mathrm{min}}$, 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 $\mathrm{CTL}_{\mathrm{min}}$ moths (0.1473 g) was 182.6% greater than that of $\mathrm{CTL}_{\mathrm{min}}$ wild-caught moths (0.0521 g). The correlation between dry weight and $\mathrm{CTL}_{\mathrm{min}}$ 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 $\mathrm{CTL}_{\mathrm{min}}$ ($R^2 = 0.0319$, adjusted $R^2 = 0.0064$, $F = 1.251$, df = 38, $P > 0.1$) or $\mathrm{CTL}_{\mathrm{max}}$ ($R^2 = 0.0038$, adjusted $R^2 = -0.0318$, $F = 0.106$, df = 28, $P > 0.1$). Lab-reared moths used in $\mathrm{CTL}_{\mathrm{min}}$

trials were 3–16 days post emergence, with an average age of 8.6 days while those used in $\mathrm{CTL}_{\max}$ trials were 1–11 days post emergence, with an average age of 8.3 days.

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

Discussion

We observed a difference in $\mathrm{CTL}_{\max}$, with lab-reared individuals demonstrating a higher maximum tolerance compared to their wild-caught counterparts. In contrast, the $\mathrm{CTL}_{\min}$ 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 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 two 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, *Helicoverpa 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.

The influence of temperature on the $\mathrm{CTL_{max}}$ of *E. auxiliaris* is further evidenced by the significant difference in $\mathrm{CTL_{max}}$ 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, Kafer 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 22–27 °C. These differences in temperature during development likely contributed to the observed variation in $\mathrm{CTL_{max}}$ 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 e.g., 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 0.3–1.3 °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 (Shah et al. 2021, Sunday et al. 2014). 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. 1998b). 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 to -5.9 °C during the summer months depending on location (Mattson et al. 1991b, White et al. 1998b, 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 days 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 3–16 days post emergence, while CTL_{max} trials included individuals 1–11 days 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 Q 2004, Almbro and Kullberg 2011).

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 (Koerwitz and Pruess 1964, O'Brien and Lindzey 1994, Kevan and Kendall 1997, White et al. 1998b). 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. 1998b). 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. 1998b, 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. 1991b). 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.

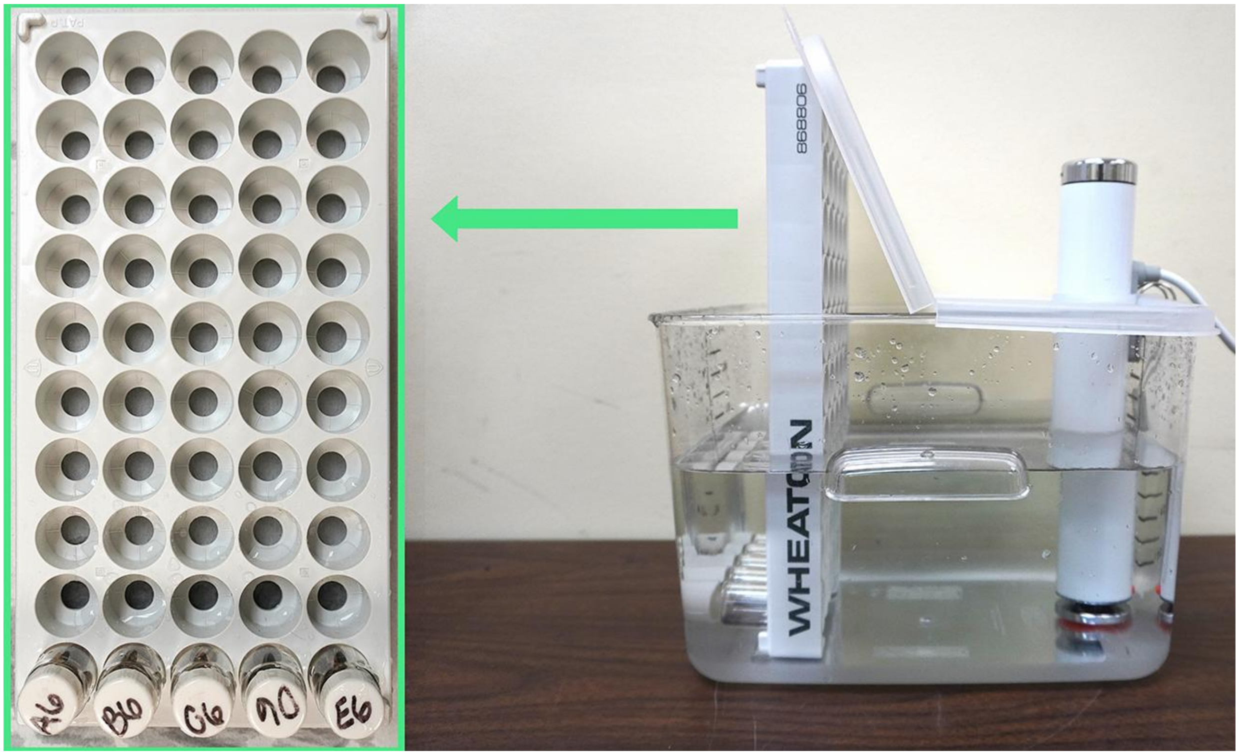

Figure 1. Critical thermal maximum (CTL$_{max}$) ramping assay. Loaded vial rack used to hold submerged subsample vials (left). Sous vide and vial rack submerged in improvised water bath (right). Individual vials each containing one moth can be seen in the bottom row of the rack.

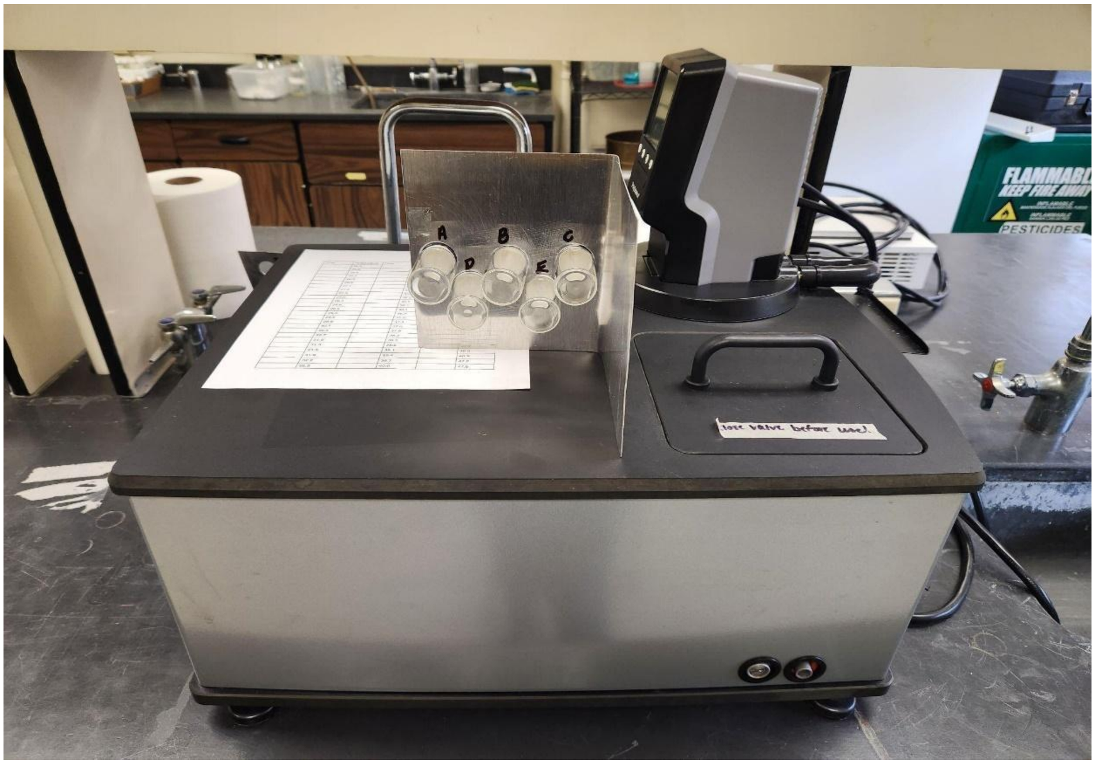

Figure 2. Critical thermal minimum (CTL_{min}) ramping assay. Individual moth vials attached to aluminum sheet shown on top of programmable water bath.

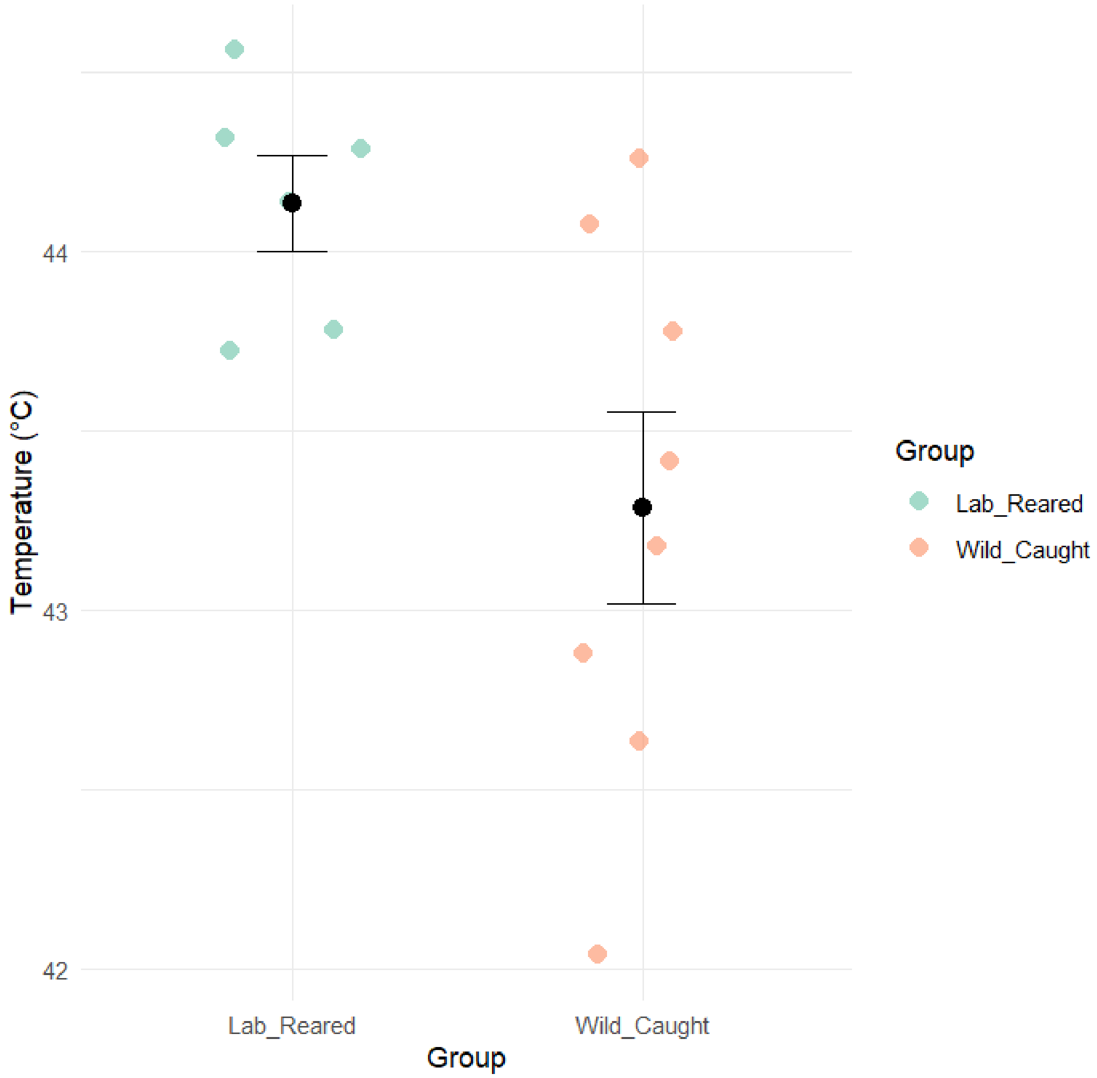

Figure 3. CTL_{max} averages for lab-reared and wild-caught *Euxoa auxiliaris* adults. Raw data points are shown as jittered dots, with each point representing a trial sample measurement for the respective group (lab-reared or wild-caught). The black dot represents the mean temperature for each group,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

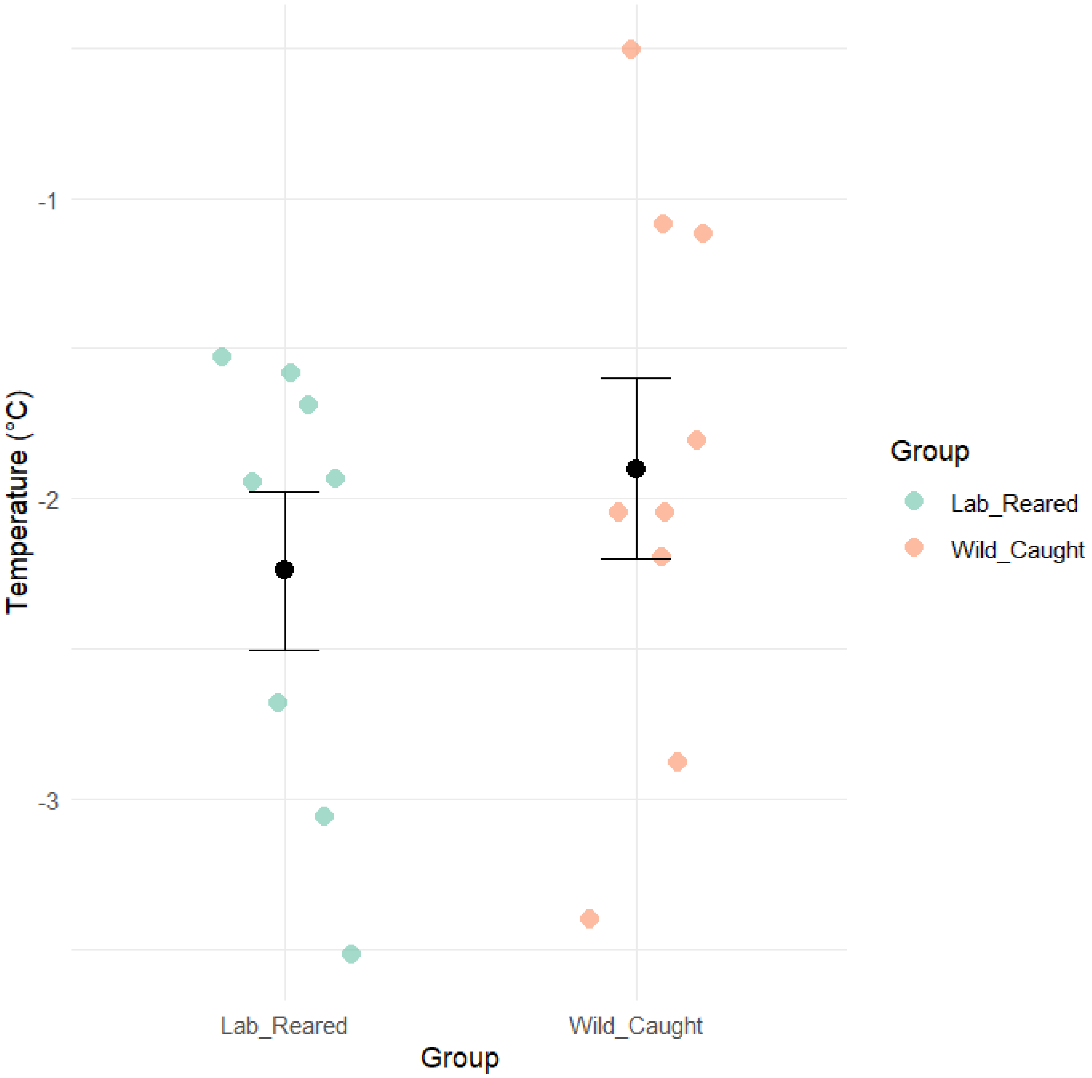

Figure 4. CTL$_{min}$ averages for lab-reared and wild-caught *Euxoa auxiliaris* adults. Raw data points are shown as jittered dots, with each point representing a trial sample measurement for the respective group (lab-reared or wild-caught). The black dot represents the mean temperature for each group,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

References

Almbro M, and Kullberg C. 2012. Weight loading and reproductive status affect the flight performance of *Pieris napi butterflies*. *Journal of Insect Behavior*. *25*: 441–452.

Arrese EL, and Soulages JL. 2010. Insect fat body: energy, metabolism, and regulation. *Annual Review of Entomology 55*(1): 207–225. https://doi.org/10.1146/annurev-ento-112408-085356

Bale JS, Masters GJ, Hodkinson ID, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology.* 8(1): 1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Bawa SA, Gregg PC, Soccoro APD, et al. 2021. Estimating the differences in critical thermal maximum and metabolic rate of *Helicoverpa punctigera* (Wallengren) (Lepidoptera: Noctuidae) across life stages. *PeerJ*. *9*. e12479. https://doi.org/10.7717/peerj.12479

Bowler K, Terblanche JS. 2008. Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? *Biological Rev*iews. *83*(3): 339–355.

Burton RL, Starks KJ, Peters DC. 1980. The army cutworm. *Bulletin-Agricultural Experiment Station, Oklahoma State University*. *Bulletin 749*:35.

Chapman JW, Reynolds DR, Wilson K. 2015. Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters. 18*(3): 287–302. https://doi.org/10.1111/ele.12407

Chapman JA, Romer JI, Stark J. 1955. Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology. 36*(1): 156–158. https://doi.org/10.2307/1931444

Chidawanyika F, Terblanche JS. 2011. Rapid thermal responses and thermal tolerance in adult codling moth *Cydia pomonella* (Lepidoptera: Tortricidae). *Journal of Insect Physiology 57*(1): 108–117. https://doi.org/10.1016/j.jinsphys.2010.09.013

Chown SL, Jumbam KR, Srensen JG, et al. 2009. Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Functional. Ecology*. *23*(1):133–140.

Chown SL, Hoffmann AA, Kristensen TN, et al. 2010. Adapting to climate change: a perspective from evolutionary physiology. *Climate Research. 43*(3): 3–15.

Crabo LG. 2018. A new genus and three new species of noctuid moths from western United States of America and Mexico (Lepidoptera, Noctuidae, Noctuinae, *Eriopygini*). *ZooKeys*. 788:183–199. https://doi.org/10.3897/zookeys.788.26068

Dittemore CM, Tyers DB, Weaver DK, et al. 2023. Using stable isotopes to determine natal origin and feeding habits of the army cutworm moth, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). *Environmental Entomology. 52*(2): 230–242. https://doi.org/10.1093/ee/nvad006

Drecktrah HG. 1978. Morphology of the internal reproductive system of the adult female army cutworm, *Euxoa auxiliaris*. *Annals of the Entomological Society of America. 71*(6): 923–927. https://doi.org/10.1093/aesa/71.6.923

French SP, French MG, Knight RR. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *Bears: Their Biology and Management. 9*: 389–399. https://doi.org/10.2307/3872725

Heinrich B. 1986. Comparative thermoregulation of four montane butterflies of different mass. *Physiological Zoology. 59*(6): 616–626. https://doi.org/10.1086/physzool.59.6.30158609

Hoffmann AA, Chown SL, Clusella-Trullas S. 2013. Upper thermal limits in terrestrial ectotherms: How constrained are they? *Functional Ecology. 27*(4): 934–949. https://doi.org/10.1111/j.1365-2435.2012.02036.x

Hoffmann AA, Sørensen JG, Loeschcke V. 2003. Adaptation of *Drosophila* to temperature extremes: Bringing together quantitative and molecular approaches. *Journal of Thermal Biology*. *28*(3): 175–216. https://doi.org/10.1016/S0306-4565(02)00057-8

Hostetler S, Whitlock C, Shuman B, et al. 2021. Greater Yellowstone climate assessment: Past, present, and future climate change in greater Yellowstone watersheds. Montana State University, Institute on Ecosystems. https://scholarworks.montana.edu/items/f1d98481-7491-4242-b3a6-8899c173b8ef

Jacobson LA, Blakeley PE. 1959. Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America. 52*(1):100–105. https://doi.org/10.1093/aesa/52.1.100

Jiménez-Pérez A, Wang Q. (2004). Effect of body weight on reproductive performance in Cnephasia jactatana (Lepidoptera: Tortricidae). *Journal of Insect Behavior*. *17*: 511–522.

Johnson SJ. 1987. Migration and the life history strategy of the fall armyworm, *Spodoptera frugiperda* in the western hemisphere. *International Journal of Tropical Insect Science. 8*(4–5–6): 543–549. doi:10.1017/S1742758400022591

Käfer H, Kovac H, Simov N, et al. 2020. Temperature tolerance and thermal environment of European seed bugs. *Insects*. *11*(3): 197. https://doi.org/10.3390/insects11030197

Kammer AE. 1970. Thoracic temperature, shivering, and flight in the monarch butterfly, *Danaus plexippus* (L.). *Zeitschrift für vergleichende Physiologie*. *68*(3): 334–344.

Kellermann V, van Heerwaarden B. 2019. Terrestrial insects and climate change: Adaptive responses in key traits. *Physiological Entomology. 44*(2): 99–115.

Kendall DM, Kevan PG, LaFontaine JD. 1981. Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist. 113*(7): 607–614. https://doi.org/10.4039/Ent113607-7

Keosentse O, Mutamiswa R, Du Plessis H, et al. 2021. Developmental stage variation in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) low temperature tolerance: Implications for overwintering. *Austral Entomology. 60*(2): 400–410. https://doi.org/10.1111/aen.12536

Kevan PG, Kendall DM. 1997. Liquid assets for fat bankers: Summer nectarivory by migratory moths in the Rocky Mountains, Colorado, USA. *Arctic and Alpine Research. 29*(4): 478–482. https://doi.org/10.1080/00040851.1997.12003268

Klok CJ, Chown SL. 1997. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* (Lepidoptera: Tineidae). *Journal of Insect Physiology*. 43(7): 685–694.

Koerwitz FL, Pruess KP. 1964. Migratory potential of the army cutworm. *Journal of the Kansas Entomological Society. 37*(3): 234–239.

Li X, Zhou Y, Wu K. 2023. Biological characteristics and energy metabolism of migrating insects. *Metabolites*. *13*(3): 439. https://doi.org/10.3390/metabo13030439

Loeschcke V, Hoffmann AA. 2007. Consequences of heat hardening on a field fitness component in *Drosophila* depend on environmental temperature. *The American Naturalist*. *169*(2): 175–183. https://doi.org/10.1086/510632

Lozano KN. 2022. Food resources for grizzly bears at army cutworm moth aggregation sites in the Greater Yellowstone Ecosystem. Master's Thesis. Montana State University, Bozeman, Montana. https://scholarworks.montana.edu/xmlui/bitstream/handle/1/16932/lozano-food-resources-2022.pdf?sequence=3

Masters AR, Malcolm SB, Brower LP. 1988. Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. *Ecology*. *69*(2): 458–467.

Mattson DJ, Gillin CM, Benson SA, et al. 1991b. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology. 69*(9): 2430–2435.

Mbande A, Mutamiswa R, Chidawanyika F. 2023. Thermal tolerance in *Spodoptera frugiperda*: Influence of age, sex, and mating status. *Scientific African. 22*. e01911. https://doi.org/10.1016/j.sciaf.2023.e01911

Mutamiswa R, Chidawanyika F, Nyamukondiwa C. 2017. Dominance of spotted stemborer *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) over indigenous stemborer species in Africa's changing climates: ecological and thermal biology perspectives. *Agricultural Forest Entomology. 19*(4): 344–356. https://doi.org/10.1111/afe.12217

Mutamiswa R, Mbande A, Nyamukondiwa C, et al. 2023. Thermal adaptation in Lepidoptera under shifting environments: Mechanisms, patterns, and consequences. *Phytoparasitica*. *51*(5): 929–955. https://doi.org/10.1007/s12600-023-01095-6

Neuvonen S, Virtanen T. 2015. Abiotic factors, climatic variability and forest insect pests. In *Climate change and insect pests.* (pp. 154–172). Wallingford UK: CABI.

Neven LG. 2000. Physiological responses of insects to heat. *Postharvest Biology Technology*. *21*(1): 103–111. https://doi.org/10.1016/S0925-5214(00)00169-1

O'Brien SL, Lindzey FG. 1998. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*. 10: 427–435.

Oregon State University. 2024. *PRISM Climate Group, Oregon State University*. https://prism.oregonstate.edu/explorer/

Parmesan C, Ryrholm N, Stefanescu C, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*. *399*(6736): 579–583.

Pepper J. 1932. Observations on a unidirectional flight of army cutworm moths and their possible bearing on aestivation. *The Canadian Entomologist. 64*(11): 241–242. https://doi.org/10.4039/Ent64241-11

Piyaphongkul J, Pritchard J, Bale J. 2014. Effects of acclimation on the thermal tolerance of the brown planthopper *Nilaparvata lugens* (S tål). *Agricultural Forest Entomology. 16*(2): 174–183. https://doi.org/10.1111/afe.12047

Pruess KP. 1963. Effects of food, temperature, and oviposition site on longevity and fecundity of the army cutworm*, Chorizagrotis Auxiliaris*. *Journal of Economic Entomology. 56*(2): 219–221. https://academic.oup.com/jee/article/56/2/219/2207489

Pruess KP. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaries* (Lepidoptera: Noctuidae). I. Evidence for a migration. *Annals of the Entomological Society of America 60*(5): 910–920.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Sgrò CM, Terblanche JS, Hoffmann AA. 2016. What can plasticity contribute to insect responses to climate change?. *Annual Review of Entomology. 61*: 433–451.

Shah AA, Woods, HA, Havird JC, et al. 2021. Temperature dependence of metabolic rate in tropical and temperate aquatic insects: Support for the climate variability hypothesis in mayflies but not stoneflies. *Global Change Biol*ogy *27*(2): 297–311. https://doi.org/10.1111/gcb.15400

Sørensen JG, Kristensen, TN, Loeschcke V., et al. 2015. No trade-off between high and low temperature tolerance in a winter acclimatized Danish *Drosophila subobscura* population. *Journal of Insect Physiology. 77*: 9–14.

Soteres KM, Berberet RC, and McNew RW. 1984. Parasites of larval *Euxoa auxiliaris* (Groté) and *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae) in Alfalfa Fields of Oklahoma. *Journal of the Kansas Entomological Society.* 57 (1): 63–68.

Stange EE, Ayres MP. 2010. Climate change impacts: Insects. *Encyclopedia of Life Sciences. 1.* https://doi.org/10.1002/9780470015902.a0022555

Sunday JM, Bates AE, Kearney MR, et al. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences. 111*(15): 5610-5615. https://doi.org/10.1073/pnas.1316145111

Taylor LR, Carter CI. 1961. The analysis of numbers and distribution in an aerial population of Macrolepidoptera. *Transactions of the Royal Entomological Society of London. 113*(12): 369–386.

Terblanche JS, Hoffmann AA, Mitchell KA, et al. 2011. Ecologically relevant measures of tolerance to potentially lethal temperatures. *Journal of Experimental Biology. 214*(22): 3713–3725. https://doi.org/10.1242/jeb.061283

Thornton PK, Ericksen PJ, Herrero M, et al. 2014. Climate variability and vulnerability to climate change: A review. *Global Change Biology. 20*(11): 3313–3328. https://doi.org/10.1111/gcb.12581

Toolson EC., & Hadley NF. 1974. Thermal tolerance of beet armyworm moths, *Spodoptera exigua*: Effects of age, temperature acclimation, and gamma radiation. *Environmental Entomology. 3*(2): 290–294. https://doi.org/10.1093/ee/3.2.290

U.S. Geological Survey. (2016, April 6). *Graph: Average temperature at Alpine weather station in Glacier NP*. U.S. Department of the Interior. https://www.usgs.gov/media/images/graph-average-temperature-alpine-weather-station-glacier-np

White D, Kendall KC, Picton, HD. 1998b. Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology. 76*(5): 835–842. https://doi.org/10.1139/z98-001

Worthen WB, Haney DC. 1999. Temperature tolerance in three mycophagous *Drosophila* species: Relationships with community structure. *Oikos*. *86*(1): 113–118. https://doi.org/10.2307/3546575

Xing K, Zhao F. 2022. Acclimation effects of natural daily temperature variation on longevity, fecundity, and thermal tolerance of the diamondback moth (*Plutella xylostella*). *Insects. 13*(4): 309. https://doi.org/10.3390/insects13040309

CHAPTER THREE

THE EFFECTS OF TEMPERATURE AND BAROMETRIC PRESSURE ON THE WINGBEAT FREQUENCY OF THE SEASONAL MIGRANT, *EUXOA AUXILIARIS* (LEPIDOPTERA: NOCTUIDAE)

Abstract

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 nine 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 data sets and contribute to the development of more accurate monitoring tools, particularly for the study of insect 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 Hoye 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 Hoye 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. 1998b, Dittemore 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. 1991b, 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 Lefkovitch 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 energy stores (O'Brien and Lindzey 1994, Kevan and Kendall 1997, White et al. 1998b). 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 16.48–60.83 Hz for some species in Noctuidae, although Lapshin and Vorontsov (2007) found that the noctuids they studied had a WBF range of 30–50 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.

Euxoa 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 non-destructively collected using pheromone traps baited with Scentry Army Cutworm Lures 12/CS (Scentry Biologicals Inc., Billings, MT, USA) in Powell, WY, USA, and from a blacklight trap (#2851A Universal Collecting System, BioQuip Products, Inc., Rancho Dominguez, CA, USA) in Bozeman, MT, USA. 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, CA, USA) for oviposition. Each cage housed 20–30 moths and was lined with paper towels for shelter. The moths were retained at ambient temperature (22–27 °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, NJ, USA). Once eggs were detected, the petri dishes were moved into vented plastic containers and stored in complete darkness at ambient temperatures of 22–27 °C until hatching occurred.

Laboratory Population Culture

Euxoa auxiliaris larvae were reared at ambient temperatures (22–27 °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, AR, USA) dispensed in 30-mL deli cups with perforated lids. The diet was replaced every 4–6 days, depending on feeding frequency and condition of diet. Pupation took place within the diet cup, and the pupae were left undisturbed for 3–4 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 25–35 pupae, which were kept in total darkness at ambient temperatures (22–27 °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 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 treatment. Treatments were temperature and pressure, with 20–21 replicates for each of nine possible temperature and pressure treatment combinations. Wingbeat frequencies were measured inside a 45-cm x 45-cm x 45-cm pressure-controlled altitude chamber (Custom, Sanatron Inc., Salt Lake City, UT, USA). The chamber was equipped with a vacuum controller (Sanatron Inc., Salt Lake City, UT, USA), 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, MT, USA) 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, GA, USA). For acoustic WBF recording, a piezoelectric microphone (ICP Microphone System, 378A06, PCB Piezotronics, Depew, NY, USA) 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, OH, USA) 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 30–60 sec), the toggle was dropped from under the standing moth to stimulate natural flight. Wingbeat frequency 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 for 30–60 sec, depending on the duration of stable flight. The recording was facilitated by a data acquisition system (cDAQ-9174, NI, Austin, TX, USA) and an Integrated Electronics Piezo-Electric (IEPE) module (NI-9230, NI, Austin, TX, USA). In cases where multiple recordings were made, the strongest signal was selected for analysis. Data were recorded at a rate of 3.2 kHz. During the experimental trial period, all aspects of the setup were determined at random, including the selection of individual moths, the temperature-pressure combinations and the number of trials conducted that day.

Data Analysis

All data were post-processed in MATLAB R2023B. To determine WBF, we converted the time series to the frequency domain via a Fast Fourier Transform (FFT) function. We subsequently calculated the frequency response magnitude from the complex FFT and applied a moving mean filter with 100 samples to the frequency response magnitude to reduce spectral noise. 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 microphone. 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 two groups exhibited non-normality, Levene’s test for homogeneity of variances was performed using ‘*leveneTest*’ function from the ‘*car*’ package which confirmed homogeneity.

We proceeded with a two-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 23.03–49.94 Hz (Fig. 3). This WBF value was the overall mean across all 191 individuals, each subjected to one of nine 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 two-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 two 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 (Fig. 5). 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 8–24 °C, highlighting the thermal effects on flight mechanics (Xu et al. 2022). Field studies of male *Choristoneura fumiferana* (Clemens) also paralleled these findings (Regniere et al. 2019). 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. 4). Pairwise comparisons revealed significant differences between 7 °C and 13 °C (mean difference = 2.86 Hz, 95% CI [1.0447, 4.6735], Tukey's HSD, $P < 0.001$), 24 °C and 7 °C (mean difference = 5.34 Hz, 95% CI [3.5016, 7.1773], Tukey's HSD, $P < 0.001$), and 24 °C and 13 °C (mean difference = 2.48 Hz, 95% CI [0.6087, 4.3521], Tukey's HSD, $P = 0.006$) (Fig 4).

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, Leger et al. 2024). 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 12–16 °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 2–5 minutes, 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 653–1013 hPa (Xu et al. 2022), 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). *Euxoa* *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).

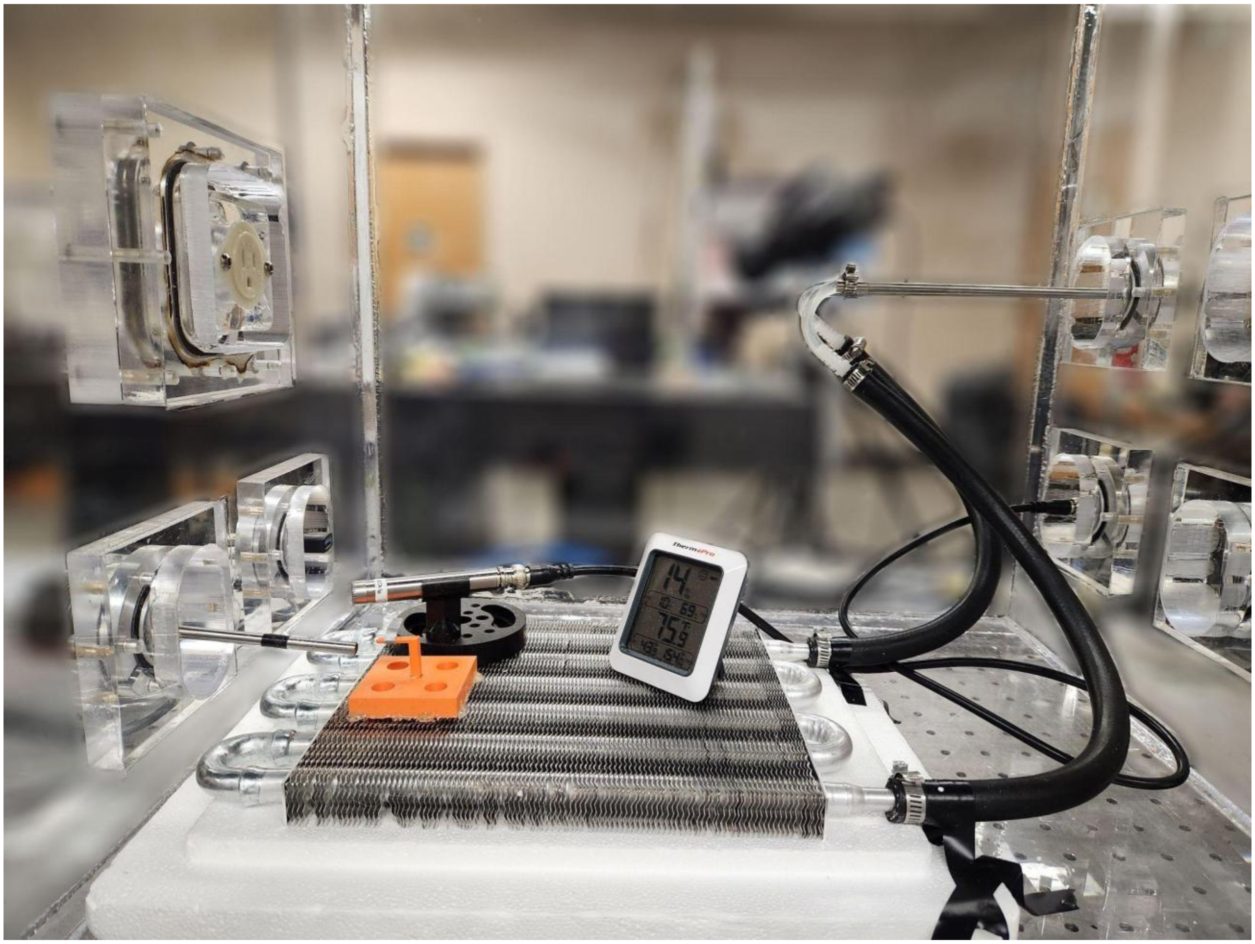

Figure 1. Experimental setup for wingbeat frequency (WBF) experiments. A chamber wall mounted toggle sits left of an orange 3-D printed stand where the moth will be attached. A piezoelectric microphone is positioned next to the toggle to record WBF. Underneath is the repurposed transmission cooling plate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

Figure 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 3-D printed stand. To the right of the moth is the piezoelectric microphone for wingbeat frequency recordings.

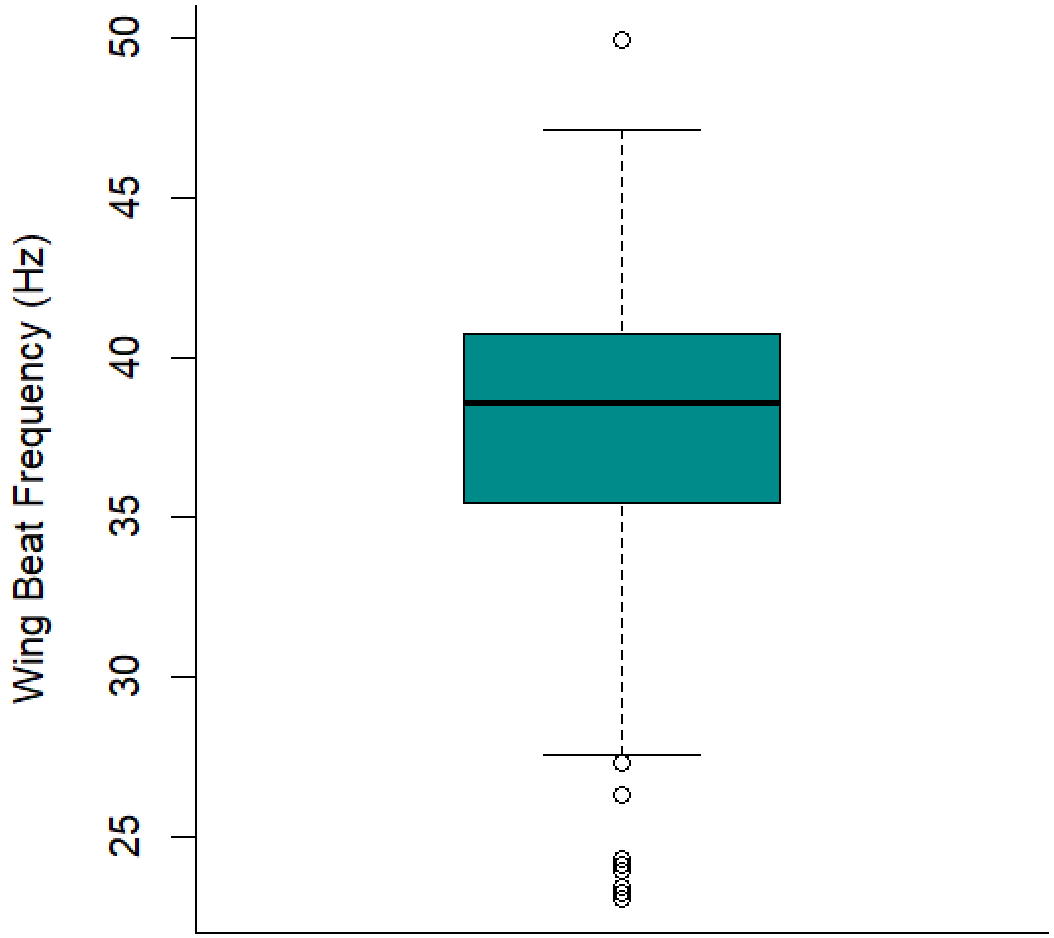

Figure 3. Wingbeat frequency of *Euxoa auxiliaris* adults over all temperatures and barometric pressures. Box represents the interquartile range, and whiskers represent the range of minimum and maximum values.

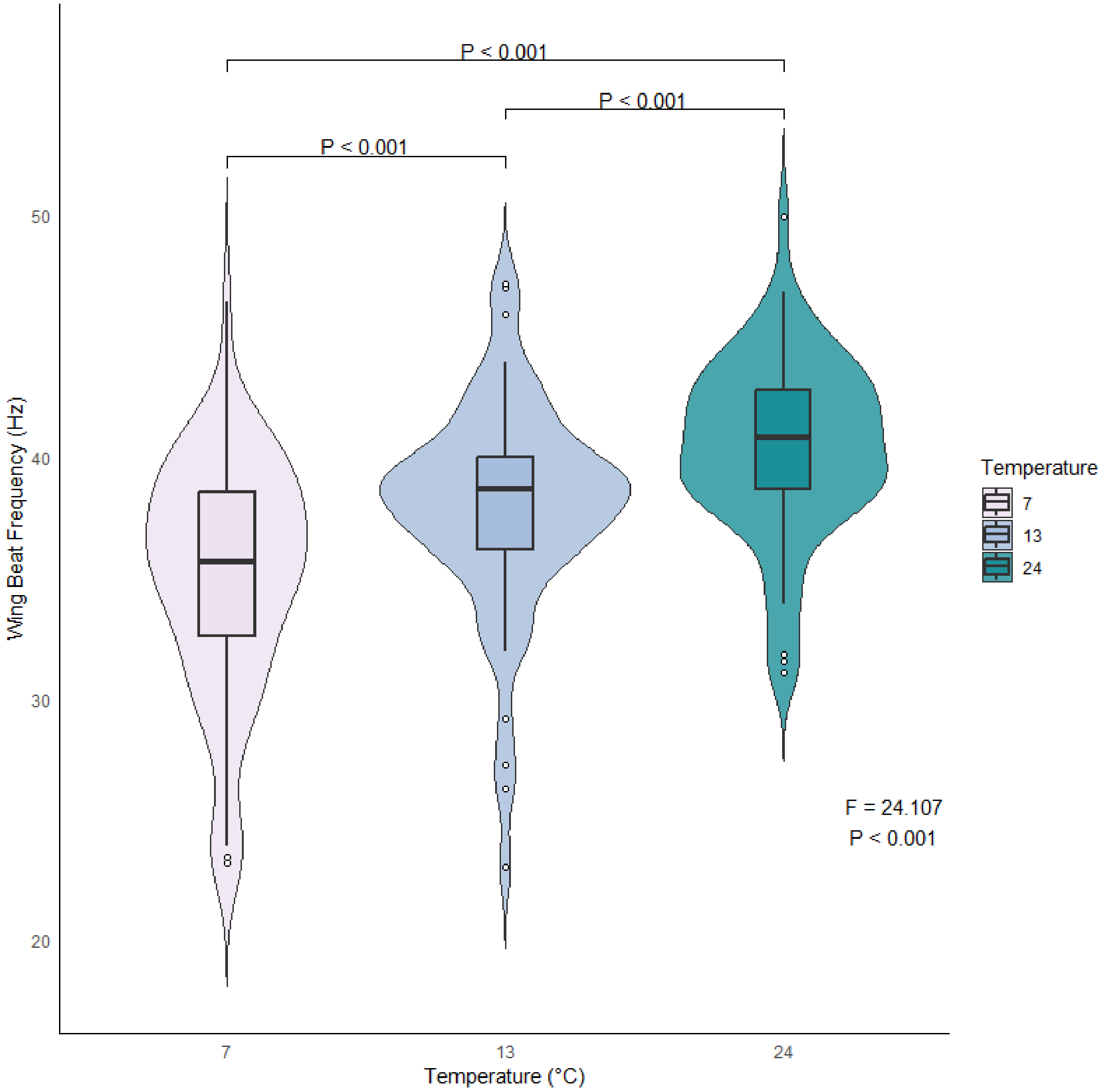

Figure 4. Violin plot showing the distribution of WBF across three temperature treatments (7, 13, and 24 °C). The violins illustrate the smoothed density of the data, while the boxplots inside each violin represent the interquartile range and median WBF. Brackets above the violins indicate significant comparisons between temperature treatments, with $P < 0.001$ for all comparisons.

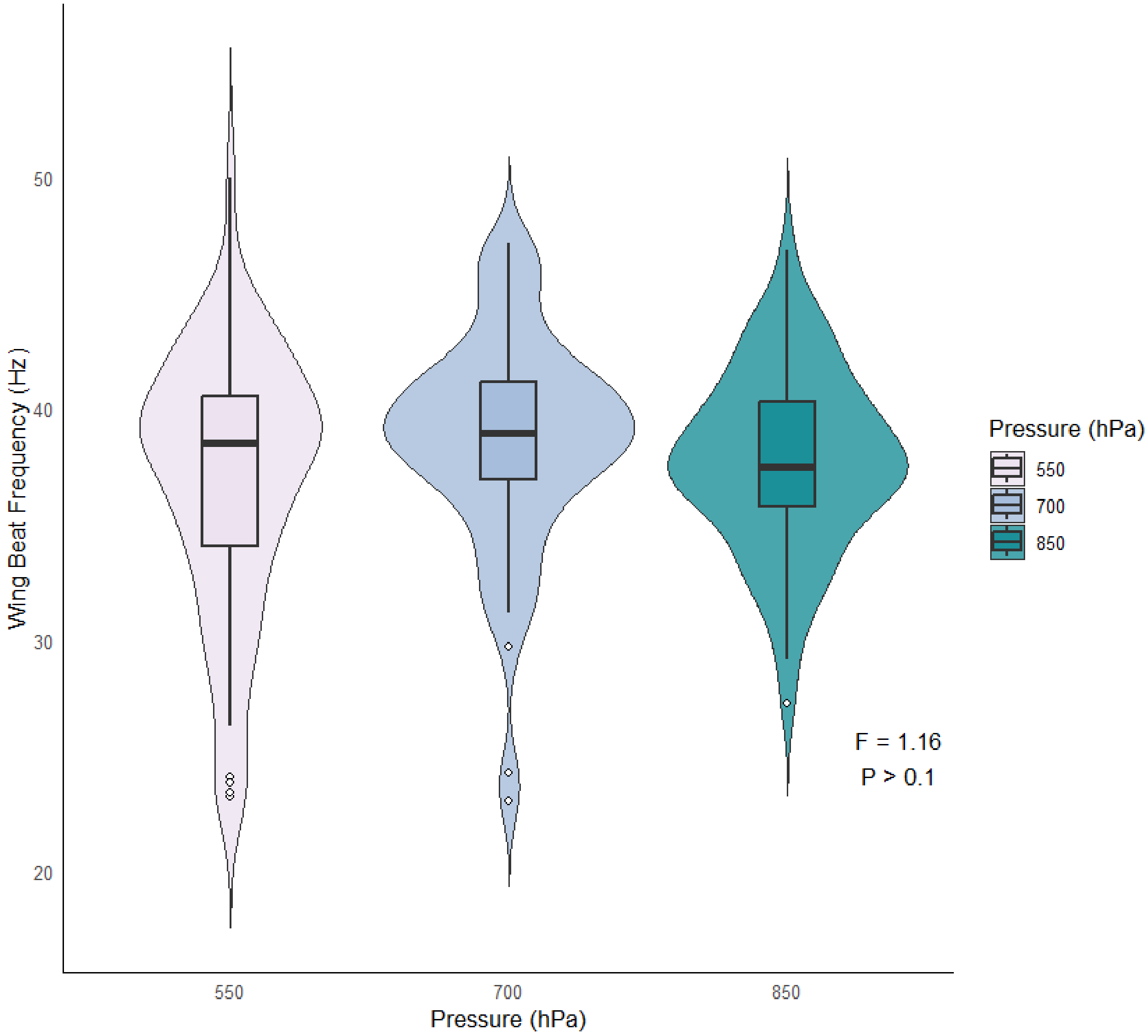

Figure 5. Violin plot showing the distribution of WBF across three pressure treatments (550, 700, and 850 hPa). The violins illustrate the smoothed density of the data, while the boxplots inside each violin represent the interquartile range and median WBF.

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 *
Pressure	73	2	36.6	1.93	> 0.1
Temperature x Pressure	112	4	28	1.47	> 0.1
Residuals	3451	182	19		

*significant relationship at $\alpha = 0.05$

References

Acar EB, Smith BN, Hansen LD, et al. 2001. Use of calorespirometry to determine effects of temperature on metabolic efficiency of an insect. *Environmental Entomology*. 30(5): 811–816. https://doi.org/10.1603/0046-225X-30.5.811

Alerstam T, Chapman JW, Bäckman J, et al. 2011. Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B: Biological Sciences*. *278*(1721): 3074–3080. https://doi.org/10.1098/rspb.2011.0058

Arrese EL, Soulages, J. L. 2010. Insect fat body: Energy, metabolism, and regulation. *Annual Review of Entomology*. *55*(1): 207–225. https://doi.org/10.1146/annurev-ento-112408-085356

Bauer S, Hoye BJ. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*. *344*(6179):1242552.

Beerwinkle KR, Lopez JD, Witz JA, et al. 1994. Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. *Environmental Entomology*. *23*(3): 676–683. https://doi.org/10.1093/ee/23.3.676

Brombacher WG. 1944. Altitude by measurement of air pressure and temperature. *Journal of the Washington Academy of Sciences*. *34*(9): 277–299. http://www.jstor.org/stable/24531101

Burton RL, Starks KJ, Peters DC. 1980. The army cutworm. *Bulletin-Agricultural Experiment Station, Oklahoma State University*. *Bulletin 749*:35.

Casey C, Cote B, Heveran CM, et al. 2025. Wing hinge dynamics influence stroke amplitudes in flapping wing insects: A frequency response approach. *bioRxiv*. 2025–01. https://doi.org/10.1101/2025.01.20.633950

Chapman JW, Drake VA, Reynolds DR. 2011. Recent insights from radar studies of insect flight. *Annual Review of Entomology*. *56*(1): 337–356. https://doi.org/10.1146/annurev-ento-120709-144820

Chapman JW, Reynolds DR, Smith AD, et al. 2002. High-altitude migration of the diamondback moth *Plutella xylostella* to the U.K.: A study using radar, aerial netting, and ground trapping. *Ecological Entomology 27*(6): 641–650. https://doi.org/10.1046/j.1365-2311.2002.00472.x

Chapman JW, Reynolds DR, Mouritsen H, et al. 2008. Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology*. *18*(7): 514–518. https://doi.org/10.1016/j.cub.2008.02.080

Chapman JW, Reynolds DR, Smith AD. 2003. Vertical-looking radar: A new tool for monitoring high-altitude insect migration. *BioScience*. *53*(5):503. https://doi.org/10.1641/0006-3568(2003)053[0503:VRANTF]2.0.CO;2

Chapman JW, Nilsson C, Lim KS, et al. 2016. Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind. *Journal of Animal Ecology*. 85(1): 115–124. https://doi.org/10.1111/1365-2656.12420

Chown SL, Gaston KJ. 2010. Body size variation in insects: A macroecological perspective. *Biological Reviews*. 85(1):139–169. https://doi.org/10.1111/j.1469-185X.2009.00097.x

Colinet H, Sinclair BJ, Vernon P, et al. 2015. Insects in fluctuating thermal environments. *Annual Review of Entomology*. 60(1): 123–140. https://doi.org/10.1146/annurev-ento-010814-021017

Dickinson MH, Lehmann FO, Sane SP. 1999. Wing rotation and the aerodynamic basis of insect flight. *Science*. *284*(5422): 1954–1960. https://doi.org/10.1126/science.284.5422.1954

Dittemore CM, Tyers DB, Weaver DK, et al. 2023. Using stable isotopes to determine natal origin and feeding habits of the army cutworm moth, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). *Environmental Entomology*. *52*:230–242. https://doi.org/10.1093/ee/nvad006

Ellington CP. 1999. The novel aerodynamics of insect flight: Applications to micro-air vehicles. *Journal of Experimental Biology*. *202*(23): 3439–3448. https://doi.org/10.1242/jeb.202.23.3439

Feng H, Wu X, Wu B, et al. 2009. Seasonal migration of *Helicoverpa armigera* (Lepidoptera: Noctuidae) over the Bohai Sea. *Journal of Economic Entomology*. *102*(1): 95–104. https://doi.org/10.1603/029.102.0114

French SP, French MG, Knight RR. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *Bears: Their Biology and Management*. *9*: 389–399. https://doi.org/10.2307/3872725

Hanski I, Pöyry J. 2007. Insect populations in fragmented habitats. In Stewart AJA, New TR, Lewis OT (Eds.) *Insect Conservation Biology: Proceedings of the Royal Entomological Society's 23rd Symposium.* CABI p. 175–202. https://doi.org/10.1079/9781845932541.0175

Hardwick DF, Lefkovitch LP. 1971. Physical and biotic factors affecting *Euxoa* species abundance in western North America: A regression analysis. *The Canadian Entomologist*. *103*(9): 1217–1235. https://doi.org/10.4039/Ent1031217-9

Heinrich B. 1981. Temperature regulation during locomotion in insects. In Herreid CF, Fourtner CR (Eds.) *Locomotion and Energetics in Arthropods* Springer. Boston MA. p 391–417. https://doi.org/10.1007/978-1-4684-4064-5_15

Kennedy TE, Sing SE, Peterson RKD. 2025. Critical thermal limits of the seasonal migrant, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). *Environmental Entomology*. nvaf019. https://doi.org/10.1093/ee/nvaf019

Kevan PG, Kendall DM. 1997. Liquid assets for fat bankers: Summer Nectarivory by migratory moths in the Rocky Mountains, Colorado, USA. *Arctic and Alpine Research. 29*:478–482. https://doi.org/10.2307/1551995

Koerwitz FL, Pruess KP. 1964. Migratory potential of the army cutworm. *Journal of the Kansas Entomological* Society. 37:234–239. https://www.jstor.org/stable/25083389

Lapshin DN, Vorontsov DD. 2007. Acoustic irradiation produced by flying moths (Lepidoptera, Noctuidae). *Entomological Review*. *87*(9): 1115–1125. https://doi.org/10.1134/S0013873807090035

Lark TJ, Spawn SA, Bougie M, et al. 2020. Cropland expansion in the United States produces marginal yields at high costs to wildlife. *Nature Communications*. *11*(1):4295. https://doi.org/10.1038/s41467-020-18045-z

Léger A, Cormier SB, Blanchard A, et al. 2024. Investigating the thermal sensitivity of key enzymes involved in the energetic metabolism of three insect species. *Journal of Experimental Biology*. *227*(10) https://doi.org/10.1242/jeb.247221

Lobell DB, Hicke JA, Asner GP, et al. 2002. Satellite estimates of productivity and light use efficiency in United States agriculture, 1982–98. *Global Change Biology*. *8*(8): 722–735. https://doi.org/10.1046/j.1365-2486.2002.00503.x

MacMillan HA, Williams CM, Staples JF, et al. 2012. Metabolism and energy supply below the critical thermal minimum of a chill-susceptible insect. *Journal of Experimental Biology*. *215*(8): 1366–1372. https://doi.org/10.1242/jeb.066381

Mattson DJ, Reid MM. 1991a. Conservation of the Yellowstone grizzly bear. *Conservation Biology*. *5*(3): 364–372. https://doi.org/10.1111/j.1523-1739.1991.tb00150.x

Mattson DJ, Gillin CM, Benson SA, et al. 1991b. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology*. *69*: 2430–2435. https://doi.org/10.1139/z91-341

McHugh ML. 2011. Multiple comparison analysis testing in ANOVA. *Biochemia Medica*. *21*(3): 203–209.

O’Brien SL, Lindzey FG. 1998. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*. *10*:427–435. https://www.jstor.org/stable/3873154

Pruess KP. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaries* (Lepidoptera: Noctuidae). I. Evidence for a migration. *Annals of the Entomological Society of America*. *60*: 910–920. https://doi.org/10.1093/aesa/60.5.910

Pruess KP, Pruess NC. 1971. Telescopic observation of the moon as a means for observing migration of the Army Cutworm, *Chorizagrotis auxiliaris* (Lepidoptera: Noctuidae). *Ecology*. *52*(6): 999–1007. https://doi.org/10.2307/1933805

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved November 22, 2024 from https://www.Rproject.org/

Reynolds DR, Chapman JW, Drake VA. 2017. Riders on the wind: The aeroecology of insect migrants. In Chilson PB, Frick WF, Kelly JF, et al. (Eds.) *Aeroecology*. p 145–178. Springer. https://doi.org/10.1007/978-3-319-68576-2_7

Régnière J, Garcia M, Saint-Amant R. 2019. Modeling migratory flight in the spruce budworm: Circadian rhythm. *Forests*. *10*(10): 877. https://doi.org/10.3390/f10100877

Régnière J, Delisle J, Sturtevant BR, et al. 2019. Modeling migratory flight in the spruce budworm: Temperature constraints. *Forests*. *10*(9): 802. https://doi.org/10.3390/f10090802

Saura S, Bastin L, Battistella L, et al. 2017. Protected areas in the world’s ecoregions: How well connected are they?. *Ecological Indicators*. *76*: 144–158. https://doi.org/10.1016/j.ecolind.2016.12.047

Stevenson RD, Josephson RK. 1990. Effects of operating frequency and temperature on mechanical power output from moth flight muscle. *Journal of Experimental Biology*. *149*(1): 61–78. https://doi.org/10.1242/jeb.149.1.61

Srygley RB, Dudley R, Hernandez EJ, et al. 2023. Quantifying the aerodynamic power required for flight and testing for adaptive wind drift in passion-vine butterflies *Heliconius sara* (Lepidoptera: Nymphalidae). *Insects*. *14*(2):112. https://doi.org/10.3390/insects14020112

Taylor GK. 2001. Mechanics and aerodynamics of insect flight control. *Biological Reviews*. *76*(4): 449–471. https://doi.org/10.1017/S1464793101005759

Taylor LR, Carter CI. 1961. The analysis of numbers and distribution in an aerial population of Macrolepidoptera. *Transactions of the Royal Entomological Society of London. 113*:369–386. https://doi.org/10.1111/j.1365-2311.1961.tb02296.x

Templeton AR, Robertson RJ, Brisson J, et al. 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Sciences of the United States of America*. *98*(10): 5426–5432. https://doi.org/10.1073/pnas.091093098

Walkden HH. 1950. Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains. *U.S. Dept. of Agriculture. 849*:19–21. Retrieved September 05, 2024 from https://www.biodiversitylibrary.org/item/130872

West JB. 1996. Prediction of barometric pressures at high altitudes with the use of model atmospheres. *Journal of Applied Physiology*. *81*(4):1850–1854. https://doi.org/10.1152/jappl.1996.81.4.1850

Westbrook JK. 2008. Noctuid migration in Texas within the nocturnal aeroecological boundary layer. *Integrative and Comparative Biology*. *48*(1): 99–106. https://doi.org/10.1093/icb/icn040

Wilcox EV. 1898. The grain aphis. An army cut-worm. *Montana Agricultural Experiment Station*, (Bulletin No. 17). https://catalog.hathitrust.org/Record/011481195

White D, Kendall KC, Picton HD. 1998b. Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology. 76*:835–842. https://doi.org/10.1139/z98-001

Wood CR, Chapman JW, Reynolds DR, et al. 2006. The influence of the atmospheric boundary layer on nocturnal layers of noctuids and other moths migrating over southern Britain. *International Journal of Biometeorology 50*(4): 193–204. https://doi.org/10.1007/s00484-005-0014-7

Xu RB, Ge SS, Yu WH, et al. 2022. Physiological and environmental influences on wingbeat frequency of Oriental Armyworm, *Mythimna separata* (Lepidoptera: Noctuidae). *Environmental Entomology*. *52*(1):1–8. https://doi.org/10.1093/ee/nvac101

Yu W, Zhou Y, Guo J, et al. 2020. Interspecific and seasonal variation in wingbeat frequency among migratory Lepidoptera in Northern China. *Journal of Economic Entomology*. *113*(5): 2134–2140. https://doi.org/10.1093/jee/toaa134

CHAPTER FOUR

FOLLOWING THE FLIGHT: USING RADAR TO TRACK THE MIGRATION OF ARMY CUTWORM MOTHS

Abstract

Seasonal migrations of insects play a vital role in maintaining ecosystem connectivity yet remain understudied at broad spatial and temporal scales. In the Greater Yellowstone Ecosystem (GYE), the army cutworm moth (*Euxoa auxiliaris*) provides a major calorie influx to alpine food webs, particularly serving as a critical food source for grizzly bears (*Ursus arctos horribilis* (L., Carnivora: Ursidae). Female grizzly bears, in particular, rely heavily on moth aggregations to meet the high energetic demands of reproduction and cub rearing. However, the migratory dynamics of *E. auxiliaris* have remained speculative until recently, when preliminary application of radar to their migration demonstrated its potential for identifying and tracking these movements. In this study, we present the first large-scale quantification of *E. auxiliaris* migration into the GYE. Using radar technology, we characterized the timing, duration, direction, and magnitude of this movement over two years and across two sites within a 4.46 km^2 front at each radar site. Results showed consistent migratory direction and orientation behavior that compensated for wind drift. These observed flight trajectories led millions of moths into alpine zones identified as moth aggregation sites, representing a substantial calorie flux into the GYE ecosystem. Together, these results demonstrate the ecological significance of *E. auxiliaris* as a nutrient transporter and emphasize the need for continued real-time monitoring to anticipate the

effects of climate and land use change along with habitat fragmentation on insect migration and in turn the reproductive success and survival of the grizzly bears that depend on them.

Introduction

The Greater Yellowstone Ecosystem (GYE) is the largest and nearly intact temperate ecosystem in the world, known for its vast wilderness, diverse topography, and rich biodiversity (Keiter 1989, Pierce et al. 2007, Debinski et al. 1999). Among its most emblematic inhabitants is the grizzly bear, (*Ursus arctos horribilis* (L., Carnivora: Ursidae), a keystone and umbrella species of conservation concern (Swanson et al. 1994, Ripple et al. 2013, Wielgus et al. 2001, Schwartz et al. 2003, Steenweg et al. 2023). The GYE supports the largest grizzly bear population in the continental United States, but conflicts with humans and livestock have intensified as bear numbers increase and their range expands (Mattson and Reid 1991a, Mattson et al. 1996, Gunther et al. 2004, Smith et al. 2024). Given these growing concerns, effective management and conservation of grizzly populations requires the preservation of habitats that provide seasonally important food sources (Noss et al. 2002, Schwartz et al. 2010, Wells et al. 2019).

Grizzlies are generalist omnivores, but rely on energy-dense foods during hyperphagia to build fat stores before hibernation (Gunther et al. 2014, Schwartz et al. 2014, Erlenbach et al. 2014, Coogan and Raubenheimer 2016). Historically, whitebark pine seeds and cutthroat trout were key calorie sources in the GYE, but both have declined considerably in recent decades due to climate change and disease (Larson and Kipfmueller 2012, Schwartz et al. 2014, Koel et al. 2005). As traditional food sources fluctuated or declined, grizzly bears adapted by shifting their foraging behavior, increasingly relying on migratory species that bring an influx of calories into the ecosystem (Mattson 1997, Hilderbrand et al. 1999a, Pease and Mattson 1999, Schwartz et al. 2003, Felicetti et al. 2003, Middleton et al. 2013, Fortin et al. 2013).

One of the most important of these species is the army cutworm moth (*Euxoa auxiliaris* Grote), a migratory insect that transports calories *en masse* into the alpine zone of the GYE (Gunther et al. 2014, Fortin et al. 2013, Mattson et al. 1991b, French et al. 1994). Each summer, *E. auxiliaris* migrates from agricultural lowlands to the Rocky Mountains, driven by the need to escape high summer temperatures and limited nectar resources in their natal habitats (Burton et al. 1980, Hardwick & Lefkovitch 1971, Pruess 1967). Upon arrival in the Rocky Mountains, the moths aggregate in massive numbers, sheltering in alpine talus during the day and foraging on alpine nectar sources at night (Burton et al. 1980, French et al. 1994, Pruess 1967). These alpine flowering communities provide the necessary energy for *E. auxiliaris* sexual maturation and return migration to natal ranges in the fall (Kevan and Kendall 1997, Pruess 1967).

In turn, moth aggregations provide a high-calorie food source for grizzly bears, which actively seek out moth sites during summer months (Mattson et al. 1991b, White et al. 1998a). A single bear can consume up to 40,000 moths per day, which at 0.5 kcal/moth is equivalent to roughly 20,000 kcal, allowing them to meet daily energy requirements during hyperphagia (Mattson et al. 1991b, French et al. 1994, White et al. 1999). This nutrient intake supports overall fat accumulation before hibernation, which may be especially critical for female grizzly bears, as their reproductive roles place particular demands on their physiology. Females must accumulate sufficient fat reserves not only for hibernation but also to support pregnancy, lactation, and early cub development (Robbins et al. 2012, Lemiere et al. 2022). These demands are compounded by the species' life history traits including delayed sexual maturity, low reproduction rates, and high cub mortality contributing to the fragility of population growth and stability as a whole (Bunnell et al. 1981, Eberhardt 2002). Because reproductive success and overall fitness are tightly linked to the nutritional condition of the mother, access to reliable, energy-dense food sources like *E. auxiliaris* aggregations may play a key role in supporting the health and reproductive potential of female bears (Eberhardt 2002, Robbins et al. 2012).

Despite its clear ecological importance, the significance of *E. auxiliaris* in the grizzly bear diet is likely underrepresented due to the inaccessibility and challenges associated with direct observation at alpine sites (Gunther et al. 2014). These logistical constraints highlight the need for alternative approaches to evaluate the moth's role in ecosystem stability, particularly by improving our understanding of its migratory and aggregation patterns.

Recent stable isotope analysis (Dittemore et al. 2023) of *E. auxiliaris* collected from alpine regions revealed a broader and more comprehensive geographic range of natal origins than previously understood (Walkden 1950, Pruess 1961, Pruess 1967, Burton et al. 1980, Michaud et al. 2006). Although these findings offer valuable insight into long-distance ecological linkages, they do not capture the dynamics of movement as they occur. Real-time tracking is needed to characterize the timing, scale, and directionality of *E. auxiliaris* migration.

Radar-based observation can provide the required spatial and temporal resolution (Chapman et al. 2003). Unlike traditional ground-based observations, radar can capture key migratory behaviors including displacement, orientation, and biomass distribution across large spatial scales (Chapman et al. 2003). Preliminary application of radar to *E. auxiliaris* migration demonstrated its potential for identifying and tracking these moth populations during migratory flight, providing a critical step toward more precisely quantifying movement patterns (Dittemore

2022). Building on this foundation, further refinement and integration of radar data with environmental variables could offer new insights into the factors shaping migration, providing a deeper understanding of how *E. auxiliaris* responds to climate change, habitat fragmentation, and other landscape-scale ecological processes, ultimately helping to safeguard the ecological connections that sustain grizzly bears, *E. auxiliaris*, and the alpine environments upon which they depend (Mattson and Reid 1991a, Schwartz et al. 2010, Watson et al. 2013).

To better understand *E. auxiliaris* migration into the GYE, we deployed two radar units along the eastern front range, where the majority of known moth aggregation sites are concentrated (Mattson et al. 1991b, Clapp et al. 2024). These radar units operated from mid-June to mid-July, covering the core migratory period. Through this targeted deployment, we were able to estimate the number of incoming moths and the corresponding calorie flux into the GYE, while also examining altitude stratification, flight direction, and orientation to further improve our understanding of *E. auxiliaris* life history and the spatial and temporal availability of this key seasonal resource for the GYE ecosystem.

Methods

Data collection

Data on *E. auxiliaris* movements were captured using portable biological radars. The deployment times, locations, and sampling strategies were chosen to simultaneously span the front range of the GYE; estimate abundance, migration height, direction, and orientation; and aid in target discrimination.

Two portable radars were deployed east of the GYE; one north of Cody, Wyoming near the Clark’s Fork Fish Hatchery (44.936 ºN, -109.137 ºW at an elevation of 1,280 m above sea level (ASL); hereafter referred to as CF), and another west of Meeteetse, Wyoming at the US Forest Service, Timber Creek Ranger Station (44.045 ºN, -109.181 ºW at an elevation of 2,451 m ASL; hereafter referred to as TC). Radars were outfitted with 1.2 m diameter parabolic antennas with a gain of 38.8 dBi. The base radar platform is a modified X-band marine radar unit (FAR 2127BB, Furuno, Camas, WA, USA), transmitting 25 kW, 0.07 µs pulses at a 3,093 pulse repetition frequency (PRF). Radars stood on a pedestal, resulting in an antenna feed height of ~2 m above ground level (AGL). Attached climate-controlled environmental enclosures housed antenna control and data capture equipment.

Data were gathered in 2023 and 2024 from mid-June to mid-July to coincide with the peak of spring *E. auxiliaris* migration (Pruess 1967, French et al. 1994). In 2023, data collection at the CF radar site occurred over two periods: June 21–July 8 and July 13–22, totaling 28 sampling days. At the TC site, sampling took place on June 18, July 1–9, and July 13–20, for a total of 18 days. The variation in the 2023 sampling periods between sites was due to logistical constraints and weather conditions that disrupted field operations. In 2024, sampling at both radar sites was conducted June 13 to July 14 for a total of 31 days.

With the antenna elevated 30° to the horizon, data were gathered using fixed-beam sampling at eight pre-defined azimuths separated by 45° (i.e., 0°, 45°, 90°, 135°, 180°, 225°, 275°, 315°). Fixed-beam sampling durations at each of these azimuths lasted ~7.15 min; a full 360° sweep was completed approximately once per hour. Fixed-beam sampling at discrete azimuths throughout a sweep 1) enables recovery of speed and direction data as a velocity-azimuth diagram (VAD) on the population of targets detected during that sweep (Browning and

Wexler 1968), while 2) increasing target dwell time within the radar beam, offering the opportunity to capture properties of targets that aid in target discrimination.

Azimuth position control was achieved using a stepper motor (24 VDC, 5 A, NEMA 23, Lin Engineering, Morgan Hill, CA, USA), with 10:1 gear ratio, in place of the stock 24 VDC motor. This gear ratio, combined with the 6:1 internal antenna gear ratio, results in a final 60:1 gear ratio between the motor and antenna, yielding an estimated 160 N·m of torque. The antenna was not protected from the environment using a radome, so high holding torque was necessary to ensure antenna position was maintained in the presence of strong winds or other unfavorable conditions. There was no evidence that the antennas lost position during operation from archived real-time position monitoring, position of the antennas on periodic inspection and decommissioning at the end of field seasons, and post-processing. Microcontroller boards (Arduino Uno R3, Arduino, Somerville, MA, USA) were used to manage antenna position under Ubuntu Linux using Arduino command line interface with motor controllers (GR214V, Geckodrive, Santa Ana, CA, USA).

Under certain circumstances, fixed-beam sampling enables capture of the wingbeat patterns of flying animals. These data may aid in target discrimination (Bruderer et al. 2010). During periods of fixed-beam sampling, radar echoes carried by the 60 MHz radar video signal were sampled at 22.5 MS/s using an analog to digital converter (PicoScope 5x44D, Pico Technology, Tyler, TX, USA). Only video samples corresponding to ≤4 km range from the radar were retained for further analysis. Targets within the max range threshold were natively sampled at the radar PRF. Signal-to-noise ratios were increased by averaging across seven pulses, resulting in an effective sampling rate of ~442 Hz on individual targets, yielding a maximum Nyquist wing beat frequency of ~221 Hz.

Target discrimination

The radars operated continuously and unattended, yielding raw datasets containing observations of flying animals as well as clutter from nearby vegetation and precipitation. The vast majority of clutter targets are rejected in real-time using a combination of azimuth-specific clutter maps and range and minimum target dwell time thresholds. Nonetheless, precipitation clutter occasionally survived these filters, especially when storm activity was severe, but was rejected during post-processing using machine learning approaches.

The XGBoost (v1.7.8.1) machine learning algorithm in R (v4.4.1) was used to identify and reject targets consistent with precipitation. Training data included precipitation and biological samples. The model was conservative, effectively identifying and rejecting precipitation targets but at the cost of some biological target rejection. Fortunately, storm activity was infrequent and localized owing to the semi-arid climate along the front range of the GYE in west-central Wyoming (Mock 1996, Shinker 2010).

Euxoa auxiliaris natural history played a considerable role in identifying targets to retain for analyses. Most *E. auxiliaris* migration occurs across the intermountain west at night between mid-June and mid-July (Pruess 1967, French et al. 1994). No other invertebrate engaging in mass migration is known to share this natural history in the vicinity of our study sites. Bird and bat migration is largely absent in June, but the early stages of fall migration begin to occur during mid-July. Consistent with this phenology, wing-beat patterns consistent with birds occurred at high altitudes as mid-July approached. These targets represented an extremely small proportion of the overall number of targets.

Biological radar targets exhibited some or all of the following: parabolic trend in received power consistent with transit of the fixed beam, range beyond that consistent with ground clutter, signal frequency spectra that do not possess strong low frequency content with asymptotically declining power (consistent with precipitation), and evidence of wing beating. At the aerial population level, aspect dependence consistent with biological targets adopting shared orientation was also frequently evident. Algorithms were developed to detect wing beat patterns for purposes of determining whether they were consistent with *E. auxiliaris* (Chapter 3) or whether vertebrate contamination might be problematic (they have not been developed into automated target discrimination algorithms). A high proportion of target records exhibited no detectable wing beat rate or pattern but were otherwise characteristic of biological targets. For this reason and given their abundance of targets and their natural history, these were counted as *E. auxiliaris*. On rare occasions, wing beat patterns were consistent with multiple targets occurring within sample volumes (e.g., Drake and Reynolds 2012) and other patterns not characteristic of vertebrates. These too were counted as *E. auxiliaris*.

Orientation

Orientation of the aerial moth population was estimated hourly from data on variation in target abundance across fixed beam samples within a sweep. This approach relies on variation in target aspect with respect to the radar, specifically that larger numbers of animals will be detected along fixed radii perpendicular to the orientation than will be detected along radii parallel to the orientation (Schmaljohann et at. 2008). The resulting variation in target abundance through a sweep approximates a sinusoid with twice the frequency of a velocity-azimuth display. Orientation can be estimated from the phase of a fitted sinusoid, but a 180° ambiguity in the estimate results owing to similar detection rates in radii parallel to the orientation, i.e., head- or tail-on detection of targets cannot be reliably determined (Drake and Reynolds 2012). We assumed orientations consistent with movement toward the GYE for the following reasons. We expect *E. auxiliaris* to orient generally toward the GYE, since high alpine habitats are their known destination, and orientations opposite this direction were strongly against the overall direction of travel. For these reasons, orientations that were 180° out of phase were adjusted accordingly.

Quantification

We estimated *E. auxiliaris* abundance through the radar coverage front for each radar station/year combination. This frontal area begins 30 m AGL, extends to a height of 1,150 m AGL and spans 3,984 m in width, equivalent to a 4.46 km^2 front. The radar beam width is target-size specific and is modeled to be 2.96° wide for *E. auxiliaris*. At this beam width, the radar is sampling 1.58% of all targets passing through the radar front. Abundance in the beam was extrapolated to the entire front by multiplying measured *E. auxiliaris* abundance by 63.14. Targets detected head- or tail-on produce weak radar echoes relative to those detected side-on, considerably reducing abundance estimates at some antenna azimuths within a sweep. Therefore, abundance estimates are conservatively adjusted to account for lower detection probability owing to target aspect by first calculating the mean of the highest four abundance estimates across all eight azimuth totals in a sweep and then applying that mean to all eight azimuths in the sweep.

Only biological targets that occurred between 2200 and 0500 daylight Mountain time were included in abundance estimates. These estimates were further constrained to include only those targets exhibiting movement toward the GYE along a front that extends from a point near Mt Maurice, Montana to the north (45.099 ºN, -109.259 ºW) and south to a location ~1.5 km east of Cottonwood Peak, Wyoming (43.819 ºN, -109.043 ºW).

Wind Regimes

To assess wind regimes during migratory flight periods, we generated wind roses using data from the Iowa Environmental Mesonet, restricted to the radar collection hours (2200–0500). Wind data were sourced from the closest ground-level weather stations, one located approximately 29 km from the CF radar site at Powell Municipal Airport (Powell, WY, USA), and another approximately 34 km from the TC radar site at a roadside weather station (WY-120, Meeteetse, WY, USA). Since localized high-altitude wind measurements were unavailable and given the topographic complexity of the region, these data may not represent high-altitude conditions but still indicate broad regional wind patterns likely influencing *E. auxiliaris* migratory routes.

Results

Across both years and sites, *E. auxiliaris* exhibited consistent flight altitude stratification (Fig.1, Table 1). Median flight height ranged from 387 to 471 m in 2023 and 394–431 m in 2024, with the interquartile range between 236–696 m AGL in 2023 and 221–633 m AGL in 2024.

Radar data revealed consistent directional preferences in *E. auxiliaris* migratory movement across sites and years, shaped by a combination of wind support and orientation.

Direction of travel differed modestly between years at each site (Table 2). At CF, the median direction of travel was strongly toward the SSW (196° in 2023, 193° in 2024), and at TC the direction of travel was generally toward the W (259° in both years). Despite interannual variability in wind patterns (Fig. 2), CF moths directions, orientations, and wind patterns were consistent across years, suggesting wind compensation by moths. At TC, direction was more variable although generally consistent toward the W, despite more variable winds than were associated with CF. Moth orientation, representing the intended heading regardless of displacement, showed a tighter clustering around SW azimuth angles (Table 3). Median moth orientation ranged from 238° to 247°, indicating that moths consistently selected SW headings even under differing wind conditions.

At the weather station near the CF site, downstream winds were predominantly SSE across both years, while at the weather station near the TC site, downstream winds were oriented NNE in 2023 and ranged from N to S through the eastern sector in 2024 (Fig. 2).

Within radar coverage areas, roughly 44 million moths entered the GYE during the 2023 sampling period (CF: 26,411,244; TC:18,155,674), and 112 million during the 2024 sampling period (CF: 47,903,940; TC: 64,355,834) (Table 4). To estimate the energetic contribution of these migrations, we used previously published values for *E. auxiliaris* body mass and caloric content upon arrival in alpine habitats. *Euxoa auxiliaris* have an arrival body mass ranging from 0.06–0.14 g, with a mean mass of 0.1 g and a caloric density of approximately 6 kcal/g (White et al. 1998b). Based on these values, the 2023 migratory pulse corresponds to an estimated energy influx of 16–37 million kcal, with a mean of 27 million kcal and in 2024, an estimated energy influx of 40–94 million kcal, with a mean of 67 million kcal (Table 5). These annual estimates are limited to the combined 4.46 km^2 fronts monitored at each radar site and do not account for the ~90 km of terrain between radar sites.

Discussion

Similar to the median altitude stratification we observed in our data, other nocturnal insect migrants have been shown to concentrate within 250–500 m AGL, an altitude range that likely offers increased atmospheric stability and favorable wind support for long-distance movement (Riley et al. 1995, Wood et al. 2006). Wind is a major factor in insect migration, influencing not only altitude selection but also energy expenditure and overall migration success (Drake and Farrow 1988, Gatehouse 1994, Gatehouse 1997).

Noctuid moths, in particular, compensate for their relatively slow inherent speeds by exploiting favorable wind currents to aid migratory movement. By selecting flight altitudes where wind speeds and directions align with their migratory objectives, they optimize both energy efficiency and travel distance (Reynolds et al. 2016, Chapman et al. 2008, Alerstam et al. 2011). For instance, the noctuid *Autographa gamma* (L.) flies at altitudes where tailwinds exceed its own flight speed, effectively reducing transportation costs (Alerstam et al. 2011). Similar wind-assisting behaviors may govern *E. auxiliaris* migration, shaping its altitude selection and movement dynamics.

Previous research on *E. auxiliaris* suggests that when facing wind resistance, these moths tend to fly at lower altitudes, indicating a sensitivity to unfavorable winds (Pruess and Pruess 1971). Altitude selection may thus serve to mitigate wind resistance, allowing for more stable flight in turbulent conditions. However, the migratory patterns we observed in *E. auxiliaris* suggest more than just atmospheric conditions as movement drivers for this species.

Beyond responding to local wind patterns, noctuid migrants are thought to rely on an inherited compass mechanism guided by visual cues and Earth's magnetic field (Chapman et al. 2008, Chapman et al. 2011b, Merlin et al. 2012). To reach their intended destinations, these moths typically select winds that facilitate movement in their preferred direction, flying downstream when conditions are favorable (Chapman et al. 2008). However, when wind patterns misalign with their intended route, noctuids employ a compass-biased downstream orientation, adjusting their heading to correct for displacement from their preferred direction of travel (Chapman et al. 2008, Chapman et al. 2011b, Dreyer et al. 2018).

A compass-biased downstream orientation could explain the discrepancy between downstream wind patterns, heading, and the migratory direction of *E. auxiliaris* observed in our results (Fig. 2, Table 2 and 3). We found that moths flew with, across, and even against prevailing winds to reach alpine aggregation sites in the GYE. This flexibility in flight behavior supports the hypothesis that *E. auxiliaris* relies on an internal compass mechanism to maintain consistent directional movement, particularly when passive transport is misaligned with their migratory goals. The repeated arrival of *E. auxiliaris* into the alpine habitats of the GYE underscores the reliability of this long-distance migration.

The ecological implications of such a consistent caloric pulse can be substantial. Cross-ecosystem energy fluxes like this can greatly affect food web dynamics and ecosystem structure (Polis et al. 1997, Barnes et al. 2018). This influx of energy-dense biomass is directly tied to the foraging strategies of grizzly bears, particularly during hyperphagia when their need to accumulate fat for hibernation drives their focus toward high-calorie foods (Lopez-Alfaro et al. 2015, Corradini et al. 2023, Clapp et al. 2024). Bears optimize fat gain by exploiting the most abundant and accessible resources (Phillips 1987, Cristescu et al. 2015). Our findings support a strong spatial overlap between moth migration patterns and concentrated bear foraging zones (Figure 3) (French et al. 1994, O'Brien and Lindzey 1998, White et al. 2017, Lozano 2022, Dittemore et al. 2023, Nunlist et al. 2023).

Although these moths are energy-rich upon their early-summer arrival, their nutritional profile changes over the course of the season. At alpine aggregation sites, *E. auxiliaris* feed nocturnally on alpine flowers, building up lipid reserves necessary for sexual maturation and their return migration to natal ranges for fall oviposition (French et al. 1994, Kevan and Kendall 1997). Through this nectar feeding, their body mass increases from a mean of approximately 0.10 g to 0.17 g, and their caloric density from approximately 6 kcal/g to 8 kcal/g by the end of the season (White et al. 1998b, Gunther et al. 2014). This progressive energy gain ultimately makes *E. auxiliaris* the most energy-dense food source among the more than 250 plant and animal species consumed by grizzly bears in the GYE (French et al. 1994, Gunther et al. 2014).

The combination of such a high caloric value, accessibility, and seasonal reliability makes *E. auxiliaris* a valuable resource for accumulating the fat reserves necessary for overwinter survival (Nelson et al. 1983, Mattson et al. 1991b, French et al. 1994, Corradini et al. 2023). This relationship takes on even greater importance for female grizzlies, whose survival and reproductive success hinges on adequate fat accumulation during hyperphagia (French et al. 1994, Robbins et al. 2012, López-Alfaro et al. 2013). Recent research suggests that females may be disproportionately dependent on moth aggregation sites, accessing them more frequently and later into the season than males (Clapp et al. 2024). This pattern implies that moth aggregation sites could play a critical role in supporting reproductive potential and population stability, underscoring the need to consider sex-specific foraging behavior in conservation strategies.

The reliance of female grizzlies on moth aggregation sites is shaped by a combination of ecological and behavioral factors, particularly those related to movement and reproductive demands. Compared to males, females have smaller home ranges, which limits their access to dispersed food sources and makes high-energy, predictable resources more valuable (Servheen 1983, Gardner et al. 2014). These constraints can be compounded by population density, which could compress female home ranges even further and intensify competition for food (Clutton-Brock and Harvey 1979, Young 1982, Mace and Waller 1997, Graham and Stenhouse 2014, Bjornlie et al. 2014). Under these conditions, *E. auxiliaris* aggregations offer a concentrated and reliable seasonal food supply for females, especially for those that are reproductive.

To successfully reproduce, female grizzlies must accumulate sufficient fat reserves before hibernation. A minimum of 25–30% body fat is required for implantation and pregnancy, with the fattest females giving birth earlier in the denning period (Robbins et al. 2012). This timing is critical, as cubs born earlier have a longer developmental period before emerging in the spring, increasing their probability of survival (Robbins et al. 2012). However, this advantage is contingent on the mother’s ability to sustain lactation throughout the winter. If her fat reserves are insufficient, she may be forced to emerge from the den early, exposing her cubs to greater risks, including starvation and infanticide (Lemiere et al. 2022).

Given the energetic demands of reproduction, particularly the need for sufficient fat reserves to support gestation and lactation through hibernation, access to high-calorie food sources like moth aggregation sites can be critical for female grizzlies. Just the small, sampled portion of airspace delivered a mean of approximately 27 million kcal (2023) and 67 million kcal (2024) at the start of summer, figures that likely fall well below the true caloric contribution by the peak of grizzly bear exploitation. Considering the limited spatial scope of our radar sampling relative to the broader scale of *E. auxiliaris* migration into the GYE, the energy influx facilitated by *E. auxiliaris* is much greater across the region.

While grizzly bears are adaptable omnivores, the nutritional contribution of *E. auxiliaris* may still offer meaningful energetic benefits during key periods. As such, changes in moth migration patterns could influence foraging behavior or energy intake. Although the broader implications remain uncertain, these potential shifts warrant consideration, especially in the context of ongoing climate-driven changes to seasonal resource patterns and overall availability (Felicetti et al. 2003, Grimm et al. 2013, Nielsen et al. 2013, Pigeon et al. 2016).

Historically, *E. auxiliaris* reached alpine habitats in mid-to-late June, concurrent with the onset of snowmelt and the start of the flowering season (Pruess 1967, French et al. 1994). However, our results suggest that this migration may occur earlier and later than measured. Data collection began on June 13, 2024, with a high frequency of moths detected immediately. Although this interpretation is based on a single season and should be approached with caution, it represents the first time an attempt was made to comprehensively document this movement (Dittemore 2022). This shift may reflect a more accurate estimate of the migration timing than previous ground-based observations or could signal broader environmental changes disrupting seasonal patterns. If *E. auxiliaris* arrives earlier, they may be encountering increasingly altered conditions at their alpine aggregation sites, with potential consequences for both the moths and the species that rely on them.

In the GYE, there is evidence of increasing temperatures in recent decades, a trend that can be particularly consequential for the high-altitude habitats where grizzly bears and *E. auxiliaris* reside (Chang and Hansen 2015, Robison 2009, Dirnböck et al. 2011). Mountain ecosystems are undergoing transformation due to decreased snowpack, shifting precipitation patterns, and rising temperatures, disrupting key ecological processes (Seastedt and Oldfather 2021, Palomo 2017, Nilsson and Grelsson 1995). In the Beartooth Plateau where *E. auxiliaris* aggregates, snowpack melt is occurring earlier, with declines in total snow accumulation and annual snow cover (Pederson et al. 2011, Tercek et al. 2015). Declining water availability in this ecosystem could have impacts on *E. auxiliaris* distribution in alpine habitats considering that known moth aggregation sites are often associated with nearby water sources, and those that dry out following snowmelt appear to be without moths (French et al. 1994). As snowpack patterns shift and drought intensifies, floral resources may become more restricted or more likely to succumb to late-season frost, threatening fragile alpine ecosystems that are already sensitive to such disturbances (Whipple and Bowser 2023, Inouye 2008, Munson and Sher 2015).

High-altitude ecosystems are characterized by a lower diversity of generalist plants compared to lower elevations, and are especially vulnerable to climate change (Ramos-Jiliberto et al. 2010, Ramos-Jiliberto et al. 2020). Pollinator networks in these environments often rely on a few key taxa, including bumblebees, flies, and moths, many of which have specialized life histories adapted to extreme conditions (Bingham and Orthner 1998, Inouye 2020). *Euxoa auxiliaris* may play an important role in sustaining these fragile floral communities by serving as a nocturnal generalist pollinator, particularly tolerant to low temperatures in alpine environments (Mattson et al. 1991b, White et al. 1998, Oregon State University 2024, Kennedy et al. 2025, Syskine and Boggs 2025). *Euxoa auxiliaris* forages on a variety of native Rocky Mountain wildflowers, include prairie bluebells (*Mertensia lanceolata*), thick-leaf ragwort (*Senecio crassulus*), mule-ears (*Wyethia amplexicaulis*), Lyall's goldenweed (*Tonestus lyallii*), and American bistort (*Bistorta bistortoides*) (Kevan and Kendall 1981, French et al. 1994). However, warming temperatures and disrupted flowering cycles can lead to phenological mismatch between plant and pollinator, potentially altering *E. auxiliaris* migratory behavior including migration patterns and range, in turn affecting the grizzly bears that rely on them (Inouye 2008, Munson and Sher 2015, Kudo 2016, Inouye 2020). As these climate-induced disruptions continue, understanding the interconnected dynamics between snowpack changes, floral resources, and pollinator behavior becomes crucial for predicting broader ecological consequences, including those affecting grizzly bears in the GYE.

This study represents the first large-scale effort to quantify the timing, scale, and duration of *E. auxiliaris* migration into the GYE, offering unprecedented insight into the scale of calorie flux these insects facilitate. These findings not only fill a longstanding knowledge gap of their migratory patterns, but this research also lays critical groundwork for future predictive modeling of their migratory behavior as well as its ecological implications. By capturing real-time movement patterns, we gain deeper insight into how this species sustains critical ecological linkages between distant ecosystems. These insights are essential not only for revealing key aspects of *E. auxiliaris* life history, but also for conserving the alpine habitats that rely on the ecological functions that migratory species provide and for conservation and management of the grizzly bear. As climate and land-use changes continue to alter migratory landscapes, such baseline data are vital for anticipating any disruptions to these systems (Hilty et al. 2012). Future research is needed to evaluate the influence of high-altitude atmospheric conditions on migratory potential and further refine data capture and analysis methods to better support target identification (Chapter 3). In addition, quantifying the return migration will allow us to evaluate the magnitude of energy flux out of the GYE which is an essential step toward fully characterizing the reciprocal nature of this unique migratory phenomenon.

Table 1. Altitude stratification (height above ground level (m AGL) of *Euxoa auxiliaris* at each radar site.

	2023		2024	
	Clark’s Fork	Timber Creek	Clark’s Fork	Timber Creek
25%	262	236	221	264
Median	471	387	394	431
75%	696	556	598	633

Table 2. Direction of travel by *Euxoa auxiliaris* in degrees azimuth relative to true north.

	2023		2024	
	Clark’s Fork	Timber Creek	Clark’s Fork	Timber Creek
25%	182	199	184	218
Median	196	259	193	259
75%	246	278	221	290

Table 3. Orientation of travel by *Euxoa auxiliaris* in degrees relative to true north.

	2023		2024	
	Clark's Fork	Timber Creek	Clark's Fork	Timber Creek
25%	216	214	215	208
Median	247	245	240	238
75%	270	273	262	272

Table 4. Estimated number of *Euxoa auxiliaris* moths passing through the 4.46 km^2 radar front during the sampling periods at each radar location and each year.

	2023	2024
Clark's Fork	26,411,244	47,903,940
Timber Creek	18,155,674	64,355,834
Total	**44,566,918**	**112,259,774**

Table 5. *Euxoa auxiliaris* energy flux into the GYE based on abundance of moths traveling into the region through a 4.46 km^2 radar front. These estimates are generated based on weight and caloric estimates for *E. auxiliaris* upon arrival to alpine habitats (French et al. 1994, White et al. 1998b).

	2023	2024
Clark’s Fork	15,846,746	28,742,364
Timber Creek	10,893,404	38,613,500
Total	**26,740,150**	**67,355,864**

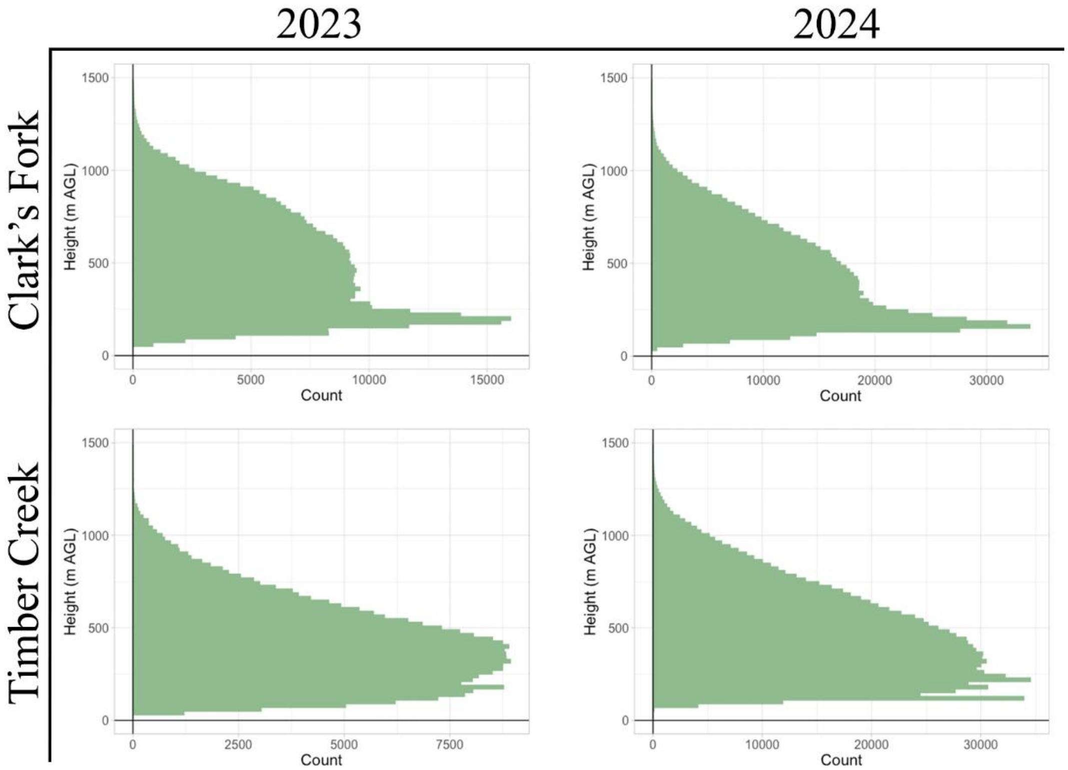

Figure 1. Altitude stratification of *Euxoa auxiliaris* detections using radar during the sampling period. The y-axis represents altitude (meters above ground level), and the x-axis indicates the number of moths detected at each altitude.

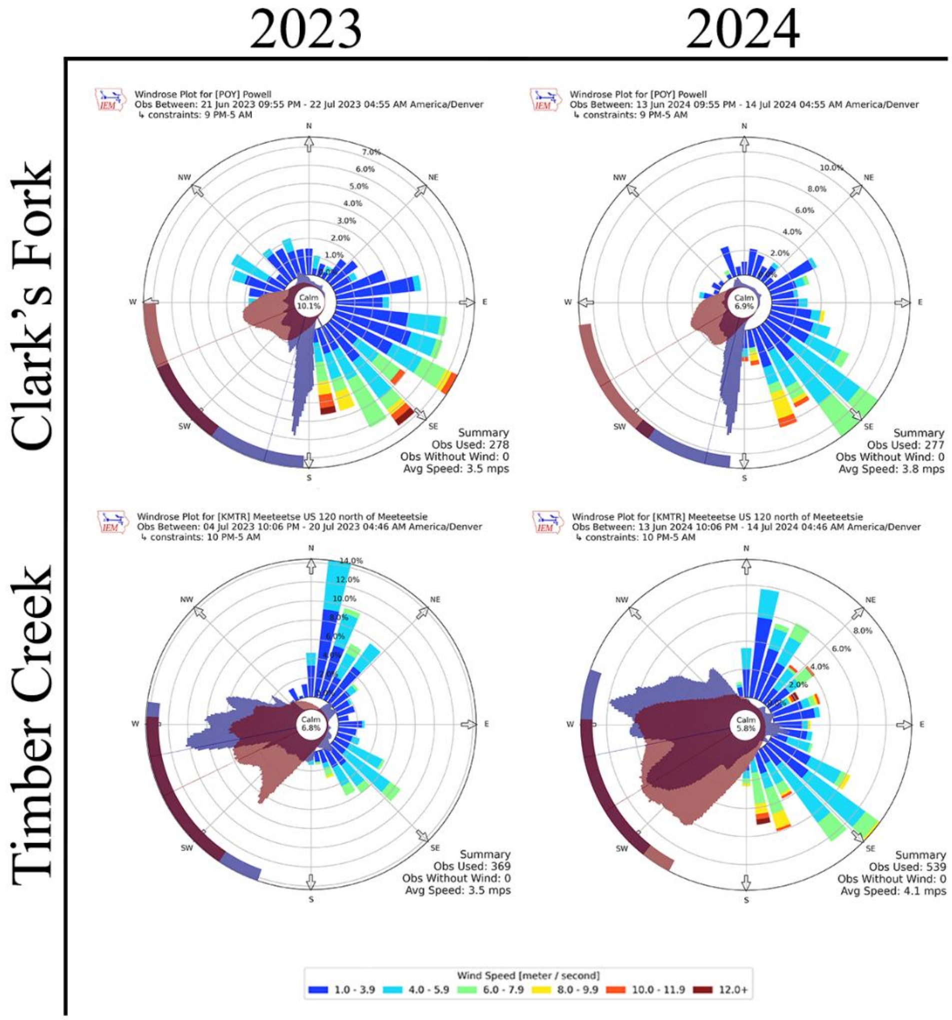

Figure 2. Direction and orientation from 2023 and 2024 sampling period of *Euxoa auxiliaris* overlaid on wind rose plots from local meteorological stations. Powell, WY station was in proximity to Clark's Fork radar site and Meeteetse, WY station was in proximity to Timber Creek radar site.

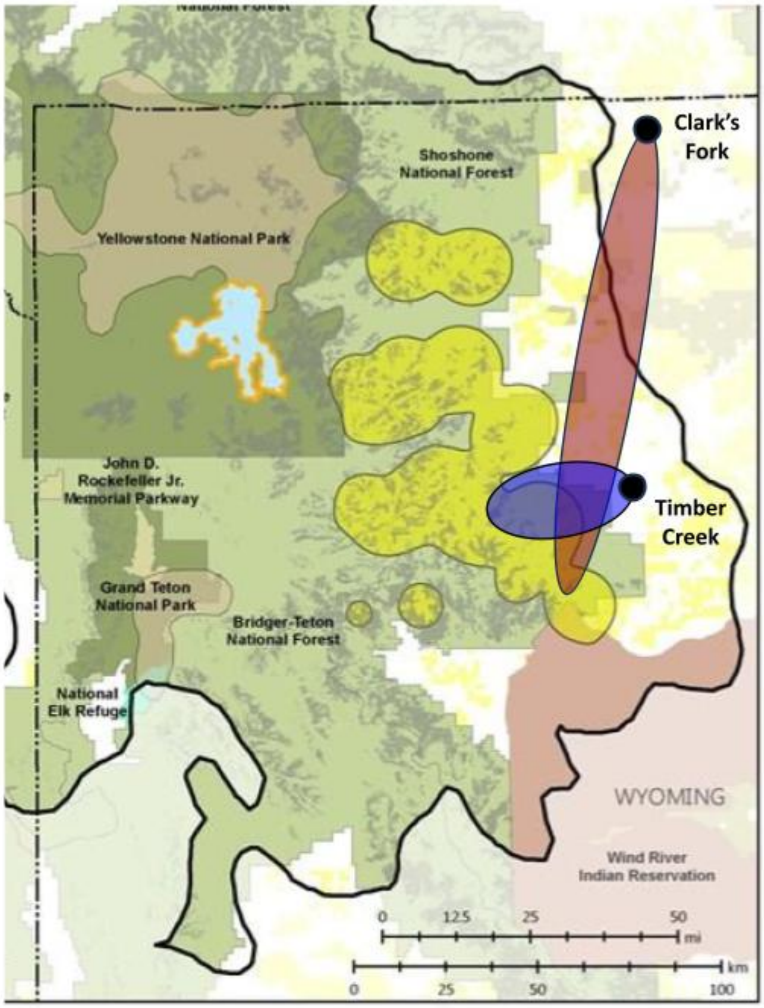

Figure 3. Broad direction pattern of movement by *Euxoa auxiliaris* into the Greater Yellowstone Ecosystem. The red oval represents movement from Clark's Fork and the blue from Timber Creek across both sampling years. Yellow areas bordered by olive green lines represent identified moth aggregation sites used by grizzly bears

References

Alerstam T, Chapman JW, Bäckman J, et al. 2011. Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B: Biological Sciences*. *278*(1721): 3074–3080. https://doi.org/10.1098/rspb.2011.0058

Barnes AD, Jochum M, Lefcheck JS, et al. 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. *Trends in ecology & evolution*. *33*(3):186–197. https://doi.org/10.1016/j.tree.2017.12.007.

Bingham RA, Orthner AR. 1998. Efficient pollination of alpine plants. *Nature*. *391*(6664): 238–239. https://doi.org/10.1038/34564

Bjornlie DD, Van Manen FT, Ebinger MR, et al. 2014. Whitebark pine, population density, and home-range size of grizzly bears in the Greater Yellowstone Ecosystem. *PloS one*. *9*(2): e88160. https://doi.org/10.1371/journal.pone.0088160

Browning KA, Wexler R. 1968. The determination of kinematic properties of a wind field using Doppler radar. *Journal of Applied meteorology and climatology*. *7*(1): 105–113. https://doi.org/10.1175/1520-0450(1968)007%3C0105:TDOKPO%3E2.0.CO;2

Bruderer B, Peter D, Boldt A. et al. 2010. Wing-beat characteristics of birds recorded with tracking radar and cine camera. *Ibis*. *152*(2): 272–291. https://doi.org/10.1111/j.1474-919X.2010.01014.x

Bunnell FL, Tait DEN, Fowler CW, et al. 1981. Population dynamics of bears—implications. *Ursus*. *13*(57). https://www.researchgate.net/profile/Fred-Bunnell/publication/306157660_Population_dynamics_of_bears-implications_for_management/links/59f657b10f7e9b553ebd29b4/Population-dynamics-of-bears-implications-for-management.pdf

Burton RL, Starks KJ, Peters DC. 1980. The army cutworm. *Bulletin-Agricultural Experiment Station, Oklahoma State University*. Bulletin *749*:35 https://openresearch.okstate.edu/server/api/core/bitstreams/cbe80810-362e-4c61-b926-9dc2929ea56e/content

Chang T, Hansen A. 2015. Historic and projected climate change in the Greater Yellowstone Ecosystem. *Yellowstone Science*. *23*(1): 14–19. https://www.researchgate.net/profile/Tony-Chang-10/publication/275345000_Historic_and_Projected_Climate_Change_in_the_Greater_Yellowstone_Ecosystem/links/55394e500cf247b858812ab2/Historic-and-Projected-Climate-Change-in-the-Greater-Yellowstone-Ecosystem.pdf#page=14

Chapman JW, Reynolds DR, Hill JK, et al. 2008. A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology*. *18*(19): R908–R909. https://doi.org/10.1016/j.cub.2008.08.014

Chapman JW, Klaassen RH, Drake VA, et al. 2011b. Animal orientation strategies for movement in flows. Current Biology. *21*(20): R861–R870. https://doi.org/10.1016/j.cub.2011.08.014

Clapp JG, Haroldson MA, Dellinger JA. 2024. *Chronology, movements, and activity of radio-marked grizzly bears using Army cutworm moth aggregation sites in the Absaroka Mountains, Shoshone National Forest, Wyoming*. Wyoming Game and Fish Department; U.S. Geological Survey

Clutton-Brock TH, Harvey PH. 1979. Comparison and adaptation. *Proceedings of the Royal Society of London. Series B. Biological Sciences*. *205*(1161): 547–565. https://doi.org/10.1098/rspb.1979.0084

Coogan SC, Raubenheimer D. 2016. Might macronutrient requirements influence grizzly bear–human conflict? Insights from nutritional geometry. *Ecosphere*. *7*(1): e01204. https://doi.org/10.1002/ecs2.1204

Corradini A, Haroldson MA, Cagnacci F, et al. 2023. Evidence for density-dependent effects on body composition of a large omnivore in a changing Greater Yellowstone Ecosystem. *Global Change Biology*. *29*(16): 4496–4510. https://doi.org/10.1111/gcb.16759

Cristescu B, Stenhouse GB, Boyce MS. 2015. Grizzly bear diet shifting on reclaimed mines. *Global Ecology and Conservation*. *4*: 207–220. https://doi.org/10.1016/j.gecco.2015.06.007

Dirnböck T, Essl F, Rabitsch W. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*. *17*(2): 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Dittemore CM. 2022. Natal Origin, Migratory Patterns, and Abundance of the Army Cutworm, *Euxoa auxiliaris*. Thesis. Montana State University, Bozeman, Montana. https://scholarworks.montana.edu/items/e08ebc9c-351c-4a11-889a-341e45c88820?show=full

Dittemore CM, Tyers DB, Weaver DK, et al. 2023. Using stable isotopes to determine natal origin and feeding habits of the army cutworm moth, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). *Environmental Entomology*. *52*(2): 230–242. https://doi.org/10.1093/ee/nvad006

Drake VA, Farrow RA. 1988. The influence of atmospheric structure and motions on insect migration. *Annual review of entomology*. *33*(1): 183–210. https://doi.org/10.1146/annurev.en.33.010188.001151

Drake VA, Reynolds DR. 2012. *Radar entomology: observing insect flight and migration*. Cabi.

Dreyer D, El Jundi B, Kishkinev D, et al. 2018. Evidence for a southward autumn migration of nocturnal noctuid moths in central Europe. *Journal of Experimental Biology*. *221*(24): jeb179218. https://doi.org/10.1242/jeb.179218

Eberhardt LL. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology*. *83*(10): 2841–2854. https://doi.org/10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2

Erlenbach JA, Rode KD, Raubenheimer D, et al. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. *Journal of Mammalogy*. *95*(1): 160–168. https://doi.org/10.1644/13-MAMM-A-161

Felicetti LA, Robbins CT, Shipley LA. 2003. Dietary protein content alters energy expenditure and composition of the mass gain in grizzly bears (*Ursus arctos horribilis*). *Physiological and Biochemical Zoology*. *76*(2): 256–261 https://doi.org/10.1139/z03-054

Fortin JK, Schwartz CC, Gunther KA, et al. 2013. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of wildlife management*. *77*(2): 270–281. https://doi.org/10.1002/jwmg.483

French SP, French MG, Knight RR. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *Bears: Their Biology and Management*. 389–399. https://doi.org/10.2307/3872725

Gardner CL, Pamperin NJ, Benson JF. 2014. Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. *Ursus*. *25*(2): 121–138. https://doi.org/10.2192/URSUS-D-14-00015.1

Gatehouse AG. 1994. Insect migration: variability and success in a capricious environment. *Population Ecology*. *36*(2): 165–171. https://doi.org/10.1007/BF02514932

Gatehouse AG. 1997. Behavior and ecological genetics of wind-borne migration by insects. *Annual review of entomology*. *42*(1): 475–502. https://doi.org/10.1146/annurev.ento.42.1.475

Graham K, Stenhouse GB. 2014. Home range, movements, and denning chronology of the grizzly bear (Ursus arctos) in west-central Alberta. *The Canadian Field-Naturalist*. *128*(3): 223–234. https://doi.org/10.22621/cfn.v128i3.1600

Grimm NB, Chapin III FS, Bierwagen B, et al. 2013. The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment*. *11*(9): 474–482. https://doi.org/10.1890/120282

Gunther KA, Haroldson MA, Frey K, et al. 2004. Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000. *Ursus*. *15*(1): 10–22. https://doi.org/10.2192/1537-6176(2004)015%3C0010:GBCITG%3E2.0.CO;2

Gunther KA, Shoemaker RR, Frey KL, et al. 2014. Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus*. *25*(1): 60–72. https://doi.org/10.2192/URSUS-D-13-00008.1

Hilderbrand GV, Jenkins SG, Schwartz CC, et al. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology*. *77*(10): 1623–1630. https://doi.org/10.1139/z99-133

Hilty JA, Lidicker Jr WZ, Merenlender AM. 2012. *Corridor ecology: the science and practice of linking landscapes for biodiversity conservation*. Island press.

Inouye DW. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*. *89*(2): 353–362. https://doi.org/10.1890/06-2128.1

Inouye DW. 2020. Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences*. *1469*(1): 26–37. https://doi.org/10.1111/nyas.14104

Iowa Environmental Mesonet. Iowa State University of Science and Technology. https://mesonet.agron.iastate.edu/

Keiter RB. 1989. Taking account of the ecosystem on the public domain: law and ecology in the Greater Yellowstone region. *U. Colo. L. Rev. 60*: 923. http://dx.doi.org/10.2139/ssrn.3534327

Kennedy TE, Sing SE, Peterson RK. 2025. Critical thermal limits of the seasonal migrant, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). *Environmental Entomology*. nvaf019. https://doi.org/10.1093/ee/nvaf019

Kendall DM, Kevan PG, LaFontaine JD. 1981. Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist*. *113*(7): 607–614. https://doi.org/10.4039/Ent113607-7

Kevan PG, Kendall DM. 1997. Liquid assets for fat bankers: Summer nectarivory by migratory moths in the Rocky Mountains, Colorado, U.S.A. *Arctic and Alpine Research*. *29*(4): 478-482. https://www.tandfonline.com/doi/abs/10.1080/00040851.1997.12003268

Koel TM, Bigelow PE, Doepke PD, et al. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries*. *30*(11): 10–19. https://doi.org/10.1577/1548-8446(2005)30[10:NLTRIY]2.0.CO;2

Kudo G. 2016. Landscape structure of flowering phenology in alpine ecosystems: significance of plant–pollinator interactions and evolutionary aspects. *Structure and function of mountain ecosystems in Japan: Biodiversity and vulnerability to climate change*. p. 41–62. https://doi.org/10.1007/978-4-431-55954-2_3

Larson ER, Kipfmueller KF. 2012. Ecological disaster or the limits of observation? Reconciling modern declines with the long-term dynamics of whitebark pine communities. *Geography Compass*. *6*(4): 189–214. https://doi.org/10.1111/j.1749-8198.2012.00481.x

Lemière L, Thiel A, Fuchs B, et al. 2022. Extrinsic and intrinsic factors drive the timing of gestation and reproductive success of Scandinavian brown bears. *Frontiers in Ecology and Evolution*. *10*: 1045331. https://doi.org/10.3389/fevo.2022.1045331

López-Alfaro C, Robbins CT, Zedrosser A, et al. 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecological Modelling*. *270*: 1–10. https://doi.org/10.1016/j.ecolmodel.2013.09.002

López-Alfaro C, Coogan SC, Robbins CT, et al. 2015. Assessing nutritional parameters of brown bear diets among ecosystems gives insight into differences among populations. *PLoS One*. *10*(6): e0128088.https://doi.org/10.1371/journal.pone.0128088

Mace RD, Waller JS. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *The Journal of Wildlife Management*. 39–52. https://www.jstor.org/stable/3802412

Mattson DJ, Reid MM. 1991a. Conservation of the Yellowstone grizzly bear. *Conservation Biology*. *5*(3): 364–372. https://doi.org/10.1111/j.1523-1739.1991.tb00150.x

Mattson DJ, Gillin CM, Benson SA, Knight RR. 1991b. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology*. *69*(9): 2430–2435. https://doi.org/10.1139/z91-341

Mattson DJ, Herrero S, Wright RG, Pease CM. 1996. Science and management of Rocky Mountain grizzly bears. *Conservation biology*. *10*(4): 1013–1025. https://doi.org/10.1046/j.1523-1739.1996.10041013.x

Mattson DJ. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation*. *81*(1-2): 161–177. https://doi.org/10.1016/S0006-3207(96)00142-5

Merlin C, Heinze S, Reppert SM. 2012. Unraveling navigational strategies in migratory insects. *Current opinion in neurobiology*. *22*(2): 353–361. https://doi.org/10.1016/j.conb.2011.11.009

Middleton AD, Morrison TA, Fortin JK, et al. 2013. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences*. *280*(1762): 20130870. https://doi.org/10.1098/rspb.2013.0870

Mock CJ. 1996. Climatic controls and spatial variations of precipitation in the western United States. *Journal of Climate*. *9*(5): 1111–1125. https://doi.org/10.1175/1520-0442(1996)009%3C1111:CCASVO%3E2.0.CO;2

Munson SM, Sher AA. 2015. Long-term shifts in the phenology of rare and endemic Rocky Mountain plants. *American journal of botany*. *102*(8): 1268–1276. https://doi.org/10.3732/ajb.1500156

Nelson RA, Folk Jr GE, Pfeiffer EW, et al. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: their biology and management*. p. 284–290. https://www.jstor.org/stable/3872551

Nielsen SE, Cattet MR, Boulanger J, et al. 2013. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. *BMC ecology*. *13*: 1–13. https://doi.org/10.1186/1472-6785-13-31

Nilsson C, Grelsson G. 1995. The fragility of ecosystems: a review. *Journal of Applied Ecology*. p. 677–692. https://doi.org/10.2307/2404808

Noss RF, Carroll C, Vance-Borland K, Wuerthner G. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology*. *16*(4): 895–908. https://doi.org/10.1046/j.1523-1739.2002.01405.x

Nunlist EA, Tyers D, Pils A, et al. 2023. Grizzly bears and humans at alpine moth sites in Wyoming, USA. *Human-Wildlife Interactions*. *17*(1): 71–85. https://www.jstor.org/stable/27316539

O'Brien SL, Lindzey FG. 1998. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*. p. 427–435. https://www.jstor.org/stable/3873154

Palomo I. 2017. Climate change impacts on ecosystem services in high mountain areas: a literature review. *Mountain Research and Development*. *37*(2): 179–187. https://doi.org/10.1659/MRD-JOURNAL-D-16-00110.1

Pease CM, Mattson DJ. 1999. Demography of the Yellowstone grizzly bears. *Ecology*. *80*(3): 957–975. https://doi.org/10.1890/0012-9658(1999)080[0957:DOTYGB]2.0.CO;2

Pederson GT, Gray ST, Woodhouse CA, et al. 2011. The unusual nature of recent snowpack declines in the North American Cordillera. *Science*. *333*(6040): 332–335. https://doi.org/10.1126/science.1201570

Pierce KL, Despain DG, Morgan LA, Good JM. 2007. The Yellowstone hotspot, greater Yellowstone ecosystem, and human geography. https://digitalcommons.unl.edu/usgspubs/79/

Pigeon KE, Stenhouse G, Côté SD. 2016. Drivers of hibernation: linking food and weather to denning behaviour of grizzly bears. *Behavioral Ecology and Sociobiology*. *70*:1745–1754. https://doi.org/10.1007/s00265-016-2180-5

Phillips MK. 1987. Behavior and habitat use of grizzly bears in northeastern Alaska. *Bears: Their Biology and Management*. 159–167. https://www.jstor.org/stable/3872622

Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual review of ecology and systematics*. *28*(1): 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

Pruess KP. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaries* (Lepidoptera: Noctuidae). I. Evidence for a migration. *Annals of the Entomological Society of America*. *60*(5): 910–920. https://doi.org/10.1093/aesa/60.5.910

Pruess KP, Pruess NC. 1971. Telescopic observation of the moon as a means for observing migration of the army cutworm, *Chorizagrotis Auxiliaris* (Lepidoptera: Noctuidae). *Ecology*. *52*(6): 999–1007. https://doi.org/10.2307/1933805

Ramos-Jiliberto R, Domínguez D, Espinoza C, et al. 2010. Topological change of Andean plant–pollinator networks along an altitudinal gradient. *Ecological Complexity*. *7*(1): 86–90. https://doi.org/10.1016/j.ecocom.2009.06.001

Ramos-Jiliberto R, Moisset de Espanés P, Vázquez DP. 2020. Pollinator declines and the stability of plant–pollinator networks. *Ecosphere*. *11*(4): e03069. https://doi.org/10.1002/ecs2.3069

Reynolds AM, Reynolds DR, Sane SP, et al. 2016. Orientation in high-flying migrant insects in relation to flows: mechanisms and strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*. *371*(1704): 20150392. https://doi.org/10.1098/rstb.2015.0392

Riley JR, Reynolds DR, Smith AD, et al. 1995. Observations of the autumn migration of the rice leaf roller *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) and other moths in eastern China. *Bulletin of Entomological Research*. *85*(3): 397–414. https://doi.org/10.1017/S0007485300036130

Robbins CT, Ben-David M, Fortin JK, et al. 2012. Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy*. *93*(2): 540–546. https://doi.org/10.1644/11-MAMM-A-155.1

Schmaljohann H, Liechti F, Bächler E, et al. 2008. Quantification of bird migration by radar–a detection probability problem. *Ibis*. *150*(2): 342–355. https://doi.org/10.1111/j.1474-919X.2007.00797.x

Schwartz CC, Miller SD, Haroldson MA. 2003. Grizzly bear. *Wild mammals of North America: biology, management, and conservation*. *2*: 556–586. https://www.researchgate.net/profile/Sterling-Miller/publication/313220567_Grizzly_bear_Ursus_arctos/links/5898e579a6fdcc32dbdd0b28/Grizzly-bear-Ursus-arctos.pdf

Schwartz CC, Haroldson MA, White GC. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *The Journal of Wildlife Management*. *74*(4): 654–667. https://doi.org/10.2193/2009-206

Schwartz CC, Fortin JK, Teisberg JE, et al. 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *The Journal of wildlife management*. *78*(1): 68–78. https://doi.org/10.1002/jwmg.633

Seastedt TR, Oldfather MF. 2021. Climate change, ecosystem processes and biological diversity responses in high elevation communities. *Climate*. *9*(5): 87. https://doi.org/10.3390/cli9050087

Servheen C. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *The Journal of Wildlife Management*. p. 1026–1035. https://www.jstor.org/stable/3808161

Shinker JJ. 2010. Visualizing spatial heterogeneity of western US climate variability. *Earth Interactions*. *14*(10): 1–15. https://doi.org/10.1175/2010EI323.1

Smith AP, Sundstrom A, Burnham M. 2024. Understanding diverse perspectives on grizzly–livestock conflict and conflict-reduction tools across southwest Montana ranching communities. *The Journal of Wildlife Management*. e22709. https://doi.org/10.1002/jwmg.22709

Steenweg R, Hebblewhite M, Burton C, et al. 2023. Testing umbrella species and food-web properties of large carnivores in the Rocky Mountains. *Biological Conservation*. *278*:

109888. https://doi.org/10.1016/j.biocon.2022.109888

Swanson CS, McCollum DW, Maj M. 1994. Insights into the economic value of grizzly bears in the Yellowstone recovery zone. *Bears: Their Biology and Management*. p. 575–582. https://doi.org/10.2307/3872746

Syskine DV, Boggs CL. 2025. Flying by night: Comparing nocturnal pollinator networks over time in the Colorado Rocky Mountains. *Ecological Entomology*. *50*(2): 235–246. https://doi.org/10.1111/een.13399

Tercek M, Rodman A, Thoma D. 2015. Trends in Yellowstone snowpack. *Yellowstone Science*. *23*(1): 20–27. https://www.researchgate.net/profile/Tony-Chang-10/publication/275345000_Historic_and_Projected_Climate_Change_in_the_Greater_Yellowstone_Ecosystem/links/55394e500cf247b858812ab2/Historic-and-Projected-Climate-Change-in-the-Greater-Yellowstone-Ecosystem.pdf#page=20

Watson JE, Iwamura T, Butt N. 2013. Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Climate Change*. *3*(11): 989–994. https://doi.org/10.1038/nclimate2007

Wells SL, McNew LB, Tyers DB, et al. 2019. Grizzly bear depredation on grazing allotments in the Yellowstone Ecosystem. *The Journal of Wildlife Management*. *83*(3): 556–566. https://doi.org/10.1002/jwmg.21618

Whipple S, Bowser G. 2023. The buzz around biodiversity decline: Detecting pollinator shifts using a systematic review. *Iscience*. *26*(11). https://doi.org/10.1016/j.isci.2023.108101

White Jr D, Kendall KC, Picton HD. 1998a. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology*. *76*(2): 221–227. https://doi.org/10.1139/z97-185

White D, Kendall KC, Picton HD. 1998b. Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology*. *76*(5): 835–842. https://doi.org/10.1139/z98-001

White Jr D, Kendall KC, Picton HD. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildlife Society Bulletin*. 146–151. https://www.jstor.org/stable/3783951

White PJ, Gunther KA, Van Manen FT, et al. 2017. Yellowstone grizzly bears: ecology and conservation of an icon of wildness. *(No Title)*. https://www.researchgate.net/publication/318324730_Yellowstone_Grizzly_Bears_Ecology_and_Conservation_of_an_Icon_of_Wildness

Wielgus RB, Sarrazin F, Ferriere R, Clobert J. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation*. *98*(3): 293–303. https://doi.org/10.1016/S0006-3207(00)00168-3

Wood CR, Chapman JW, Reynolds DR, et al. 2006. The influence of the atmospheric boundary layer on nocturnal layers of noctuids and other moths migrating over southern Britain. *International Journal of Biometeorology*. 50(4): 193–204. https://doi.org/10.1007/s00484-005-0014-7

Young BF, Ruff RL.1982. Population-dynamics and movements of black bears in east central Alberta. *Journal of Wildlife Management* 46: 845–860. https://www.jstor.org/stable/3808217

CHAPTER FIVE

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Summary

The purpose of our project was to increase our understanding of the migration of *Euxoa auxiliaris* to improve the management of grizzly bears in the Rocky Mountains, as well as ecosystem management. Here, we summarize our findings and management recommendations.

Critical thermal limits

Our primary objective was to determine the upper and lower critical thermal limits (CTL_{max} and CTL_{min}) of *E. auxiliaris* using a ramping tolerance assay. Although it was known that *E. auxiliaris* migrate to alpine moth aggregation sites to escape the high summer temperatures and limited nectar supply in their natal range, the ecological implications of their thermal tolerance are not well understood. By examining their thermal limits, we aimed to provide insights into the species' thermal biology, which would help predict climate change impacts on their range distribution and, consequently, the availability of this important food source for grizzly bears.

The CTL_{max} was unsurprising, falling within a range typical for temperate Lepidoptera. In contrast, the CTL_{min} was notably low for lepidopteran species, which aligns with expectation because *E. auxiliaris* spends most of its adult life in alpine habitats. These findings suggest a potential adaptability that may enable *E. auxiliaris* to persist under shifting environmental conditions. Their relatively low cold tolerance supports survival in cooler climates, while their CTL_{max} indicates they may also tolerate warming temperatures to a certain degree. During rearing for this and other experiments, individuals tolerated temperatures around 20 °C, suggesting some degree of thermal plasticity. However, further research is needed to assess survival under high and variable temperatures that more closely reflect natural environmental conditions as well as the influence of age on thermal tolerance, which has been found to impact this variable but was not observed in this study.

Wingbeat frequency

Given the ambiguity associated with species identification when using radar, we aimed to supplement radar data with a wingbeat frequency (WBF) study—particularly under controlled temperature and pressure conditions—to better attribute radar-detected signals to specific species without direct confirmation. Radar is capable of providing insights into the WBF of target signals during flight (Chapman et al. 2003), but environmental conditions can affect signal interpretation.

We tested nine combinations of air temperature (7, 13, 24 °C) and barometric pressure (550, 700, 850 hPa), reflecting conditions commonly encountered by migrating moths at altitudes associated with mass movement. Our results showed that temperature significantly influenced WBF: mean values were 35.08 Hz at 7 °C, 37.94 Hz at 13 °C, and 40.42 Hz at 24 °C. In contrast, barometric pressure did not have a significant effect. Across all 191 individuals sampled, mean WBF was approximately 37.07 Hz, with a range of 23.03 to 49.94 Hz. Although these findings on the effects of temperature and pressure on WBF align with previous studies in other Lepidoptera, they provide valuable species-specific context for radar signal interpretation.

There were, however, limitations in this study, most notably in temperature control. Our pressure–controlled altitude chamber lacked sufficient equipment for precise temperature regulation, which increased trial duration and limited the exposure time of individuals to consistent temperature treatments. Future iterations of this study would benefit from improved temperature control, especially at lower temperature thresholds, as well as incorporating free-flight trials to better simulate natural conditions. Additionally, considering the known influence of wind on insect flight control and optimization, it would be worthwhile to explore the combined effects of wind and temperature on WBF. This would, however, require a redesign of the acoustic data collection method to account for the additional noise interference introduced by wind.

Quantifying abundance using radar

Quantifying the abundance of *E. auxiliaris* at aggregation sites presents numerous challenges due to the behavior of both moths and grizzly bears, as well as the inaccessibility of high-elevation habitats, which together makes direct population assessments difficult. To overcome these obstacles, we employed radar technology to not only estimate moth abundance, and, by extension, the associated calorie flux into the GYE, but also to improve our understanding of moth migratory behavior. This approach increases our understanding of the ecological connection between the GYE and the natal ranges of *E. auxiliaris*, and it provides valuable insight for improving grizzly bear management and conservation efforts within the region.

Radar observation proved highly effective in characterizing the movement patterns and estimating abundance of *E. auxiliaris* during the spring migration. We found that moths were heavily concentrated between 387 and 471 m above ground level (AGL), with movement consistently oriented in a southerly direction from the Clark’s Fork (CF) radar site and in a westerly direction from the Timber Creek (TC) site. These directional patterns along with the relationship between orientation, direction of travel, and prevailing winds suggest that *E. auxiliaris* may use a compass-based navigational mechanism to reach the alpine habitats of the GYE. However, in the absence of high-altitude meteorological data, this interpretation is based on ground-level weather observations and should be viewed as preliminary.

Radar-based quantification of migratory movements from each site enabled us to estimate that approximately 44 million moths entered the eastern front range of the GYE during the 2023 sampling period (CF: 26,411,244, TC:18,155,674), and roughly 112 million during the 2024 sampling period (CF: 47,903,940, TC: 64,355,834). These abundance estimates translate to an annual calorie flux of approximately 267 million in 2023 and 673 million calories in 2024. It is important to note that these values likely represent a very conservative estimate, as we did not extrapolate or interpolate between the two radar sites, which are spaced roughly 90 km apart, meaning these findings are based on a 4.46 km^2 front at each site.

We concluded that the majority of our abundance estimates likely reflect *E. auxiliaris*, based on the species' well documented life history and the lack of other major migratory movements during the spring migration period. But to further support target attribution, we intended to incorporate WBF data; however, the analysis proved more challenging than anticipated. Refining WBF measurement techniques would be particularly valuable in future efforts to quantify the outgoing migration from the GYE, which temporally overlaps with other migratory species events. Improved WBF data could help distinguish *E. auxiliaris* from other species with distinct flight signatures, ultimately allowing for more precise abundance estimates.

Management recommendations

Critical thermal limits

Euxoa auxiliaris seem to be well adapted to cold environments, exhibiting critical thermal limits that reflect its prolonged residence in alpine habitats. This physiological resistance suggests that this species possesses a degree of thermal plasticity, supported also by the environmental conditions in which they tolerate in alpine habitats with documented temperature exposure ranging from 40 °C to below freezing (French et al. 1994).

Considering these environmental temperatures and no evidence of immediate population-level stress related to thermal limits, we do not currently indicate a need for management intervention. However, there is room for additional research on the thermal tolerance and adaptability in a field setting to elucidate moth behavior and potential effects on grizzly bear feeding.

Wingbeat frequency

We recommend that wingbeat frequency be tested under wind conditions to enhance our understanding of the flight dynamics of *E. auxiliaris* as well as the interpretation and utility of radar for monitoring the migratory behavior of the species. Beyond investigating this additional variable, we do not see a need for additional management intervention.

Quantifying abundance using radar

Our radar findings revealed a high density of *E. auxiliaris* at the onset of our data collection period, suggesting that a portion of the migration had already occurred. Based on this, we recommend initiating radar monitoring at the beginning of June to better capture the full scope of the incoming migration. Earlier data collection would improve abundance estimates and provide a more complete picture of seasonal movement patterns.

To further improve accuracy, we recommend deploying additional radar units across the eastern front range of the GYE. A broader spatial distribution of radar coverage would allow for improved detection of migratory flux and support more robust extrapolation of abundance across the landscape. These units could also be leveraged to quantify the outgoing migration, which typically occurs from mid-August to mid-September. However, fall migration can be complicated by overlapping insect and bird migrations requiring refinement in data interpretation, particularly regarding WBF. Improved classification of WBF signatures would enhance our ability to attribute target signals to *E. auxiliaris* with greater confidence, making radar a more powerful tool for both incoming and outgoing migration quantification.

Another key limitation both in tracking *E. auxiliaris* migration and accurately modeling their movement patterns is the availability of meteorological data, particularly at high altitudes. In our study, we relied solely on ground-based meteorological observation, which likely does not fully reflect the atmospheric conditions experienced by moths during flight, especially given that movement was most concentrated between 387-471 m AGL. Atmospheric variables such as wind speed, direction, and temperature at flight altitude can influence orientation, direction, and overall migratory efficiency, which are factors that are well-documented in aerial insect migrations. The absence of high-altitude meteorological data restricted our ability to fully interpret the mechanisms driving observed flight patterns and behavioral orientation. We recommend integrating upper-atmosphere data collection, such as through weather balloons, lidar, or satellite-linked systems, into future research. Doing so would offer critical insights into the spatial and temporal distribution of *E. auxiliaris*, improving predictive models of migratory behavior, and help assess how shifting climatic conditions may alter these patterns over time.

Establishing long-term radar-based monitoring would be especially valuable in providing insights into population trends, migratory timing, and spatial distribution. Over time, this monitoring could help identify the effects of climate change and landscape changes on *E. auxiliaris* movement patterns which would contribute to a better understanding of the interconnectedness of these regions as well as the availability of *E. auxiliaris* abundance and reliability of this critical high-calorie food resource for grizzly bears. All of this information would be essential for improving management and conservation planning in the GYE.

References

Chapman JW, Reynolds DR, Smith AD. 2003. Vertical-looking radar: A new tool for monitoring high-altitude insect migration. *BioScience. 53*(5):503–511. https://doi.org/10.1641/0006-3568(2003)053[0503:VRANTF]2.0.CO;2

French SP, French MG, Knight RR. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. Bears: *Their Biology and Management. 9*: 389–399. https://doi.org/10.2307/3872725

CUMULATIVE REFERENCES CITED

Acar EB, Smith BN, Hansen LD, et al. 2001. Use of calorespirometry to determine effects of temperature on metabolic efficiency of an insect. *Environmental Entomology 30*(5): 811–816. https://doi.org/10.1603/0046-225X-30.5.811

Alerstam T, Chapman JW, Bäckman J, et al. 2011. Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B: Biological Sciences*. *278*(1721): 3074–3080. https://doi.org/10.1098/rspb.2011.0058

Almbro M, and Kullberg C. 2012. Weight loading and reproductive status affect the flight performance of Pieris napi butterflies. *Journal of Insect Beha*vior. *25*: 441-452.

Arrese EL, Soulages JL. 2010. Insect fat body: energy, metabolism, and regulation. *Annual Review of Entomology*. 55(1): 207–225. https://doi.org/10.1146/annurev-ento-112408-085356

Arritt R. W, Rink TD, Segal M, et al. 1997. The Great Plains low-level jet during the warm season of 1993. *Monthly Weather Review. 125*(9): 2176–2192. https://doi.org/10.1175/1520 0493(1997)125%3C2176:TGPLLJ%3E2.0.CO;2

Bale JS, Masters GJ, Hodkinson ID, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology. 8*(1): 1-16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Barnes AD, Jochum M, Lefcheck JS, et al. 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. *Trends in ecology & evolution. 33*(3):186–197. https://doi.org/10.1016/j.tree.2017.12.007

Bauer S, Hoye BJ. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science. 344*(6179):1242552. https://doi.org/10.1126/science.1242552

Bawa SA, Gregg PC, Soccoro APD, et al. 2021. Estimating the differences in critical thermal maximum and metabolic rate of Helicoverpa punctigera (Wallengren) (Lepidoptera: Noctuidae) across life stages. *PeerJ.* 9:e12479. https://doi.org/10.7717/peerj.12479

Beerwinkle KR, Lopez JR JD, Witz JA, et al. 1994. Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. *Environmental Entomology. 23*(3): 676–683. https://doi.org/10.1093/ee/23.3.676

Beirne BP. 1970. Effects of precipitation on crop insects. *The Canadian Entomologist. 102*(11): 1360–1373. https://doi.org/10.4039/Ent1021360-11

Bingham RA, Orthner AR. 1998. Efficient pollination of alpine plants. *Nature. 391*(6664): 238–239. https://doi.org/10.1038/34564

Bjornlie DD, Van Manen FT, Ebinger MR, et al. 2014. Whitebark pine, population density, and home-range size of grizzly bears in the Greater Yellowstone Ecosystem. *PloS one. 9*(2): e88160. https://doi.org/10.1371/journal.pone.0088160

Bowler K, Terblanche JS. 2008. Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? *Biological Reviews. 83*(3): 339-355.

Brombacher WG. 1944. Altitude by measurement of air pressure and temperature. *Journal of the Washington Academy of Sciences. 34*(9): 277–299. http://www.jstor.org/stable/24531101

Browning KA, Wexler R. 1968. The determination of kinematic properties of a wind field using Doppler radar. *Journal of Applied meteorology and climatology. 7*(1): 105–113. https://doi.org/10.1175/1520-0450(1968)007%3C0105:TDOKPO%3E2.0.CO;2

Bruderer B, Peter D, Boldt A. et al. 2010. Wing-beat characteristics of birds recorded with tracking radar and cine camera. *Ibis. 152*(2): 272–291. https://doi.org/10.1111/j.1474-919X.2010.01014.x

Bunnell FL, Tait DEN, Fowler CW, et al. 1981. Population dynamics of bears—implications. *Ursus. 13*(57). https://www.researchgate.net/profile/Fred-Bunnell/publication/306157660_Population_dynamics_of_bears-implications_for_management/links/59f657b10f7e9b553ebd29b4/Population-dynamics-of-bears-implications-for-management.pdf

Burton RL, Starks KJ, Peters DC. 1980. The army cutworm. Bulletin-Agricultural Experiment Station, Oklahoma State University. Bulletin 749:35 https://openresearch.okstate.edu/server/api/core/bitstreams/cbe80810-362e-4c61-b926-9dc2929ea56e/content

Casey C, Cote B, Heveran CM, et al. 2025. Wing hinge dynamics influence stroke amplitudes in flapping wing insects: A frequency response approach. *bioRxiv*. 2025–01. https://doi.org/10.1101/2025.01.20.633950

Chang T, Hansen A. 2015. Historic and projected climate change in the Greater Yellowstone Ecosystem. *Yellowstone Science. 23*(1): 14–19. https://www.researchgate.net/profile/Tony-Chang10/publication/275345000_Historic_and_Projected_Climate_Change_in_the_Greater_Yellowstone_Ecosystem/links/55394e500cf247b858812ab2/Historic-and-Projected-Climate-Change-in-the-Greater-Yellowstone-Ecosystem.pdf#page=14

Chapman JW, Reynolds DR, Wilson K. 2015. Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters. 18*(3): 287–302. https://doi.org/10.1111/ele.12407

Chapman JA, Romer JI, Stark J. 1955. Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology. 36*(1): 156–158. https://doi.org/10.2307/1931444

Chapman JW, Reynolds DR, Hill JK, et al. 2008. A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology. 18*(19): R908–R909. https://doi.org/10.1016/j.cub.2008.08.014

Chapman JW, Klaassen RH, Drake VA, et al. 2011b. Animal orientation strategies for movement in flows. *Current Biology. 21*(20): R861–R870. https://doi.org/10.1016/j.cub.2011.08.014

Chapman JW, Drake VA, Reynolds DR. 2011a. Recent insights from radar studies of insect flight. *Annual Review of Entomology. 56*(1): 337–356. https://doi.org/10.1146/annurev-ento-120709-144820

Chapman JW, Reynolds DR, Smith AD, et al. 2002. High-altitude migration of the diamondback moth Plutella xylostella to the U.K.: A study using radar, aerial netting, and ground trapping. *Ecological Entomology. 27*(6): 641–650. https://doi.org/10.1046/j.1365-2311.2002.00472.x

Chapman JW, Reynolds DR, Smith AD. 2003. Vertical-looking radar: A new tool for monitoring high-altitude insect migration. *BioScience. 53*(5):503–511. https://doi.org/10.1641/0006-3568(2003)053[0503:VRANTF]2.0.CO;2

Chapman JW, Reynolds DR, Mouritsen H, et al. 2008. Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology. 18*(7): 514–518. https://doi.org/10.1016/j.cub.2008.02.080

Chapman JW, Nilsson C, Lim KS, et al. 2016. Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind. *Journal of Animal Ecology. 85*(1): 115–124. https://doi.org/10.1111/1365-2656.12420

Chidawanyika F, Terblanche JS. 2011. Rapid thermal responses and thermal tolerance in adult codling moth *Cydia pomonella* (Lepidoptera: Tortricidae). *Journal of Insect Physiology. 57(*1): 108–117. https://doi.org/10.1016/j.jinsphys.2010.09.013

Chown SL, Jumbam KR, Srensen JG, et al. 2009. Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Functional Ecology. 23*(1):133–140.

Chown SL, Hoffmann AA, Kristensen TN, et al. 2010. Adapting to climate change: a perspective from evolutionary physiology. *Climate Research. 43*(3): 3–15. https://doi.org/10.3354/cr00879

Chown SL, Gaston KJ. 2010. Body size variation in insects: A macroecological perspective. *Biological Reviews. 85*(1):139–169. https://doi.org/10.1111/j.1469-185X.2009.00097.x

Clapp JG, Haroldson MA, Dellinger JA. 2024. *Chronology, movements, and activity of radio-marked grizzly bears using Army cutworm moth aggregation sites in the Absaroka Mountains, Shoshone National Forest, Wyoming*. Wyoming Game and Fish Department; U.S. Geological Survey

Clutton-Brock TH, Harvey PH. 1979. Comparison and adaptation. *Proceedings of the Royal Society of London. Series B. Biological Sciences. 205*(1161): 547–565. https://doi.org/10.1098/rspb.1979.0084

Colinet H, Sinclair BJ, Vernon P, et al. 2015. Insects in fluctuating thermal environments. *Annual Review of Entomology. 60*(1): 123–140. https://doi.org/10.1146/annurev-ento-010814-021017

Coogan SC, Raubenheimer D. 2016. Might macronutrient requirements influence grizzly bear–human conflict? Insights from nutritional geometry. *Ecosphere. 7*(1): e01204. https://doi.org/10.1002/ecs2.1204

Cooley RA. 1916. Observations on the life history of the army cutworm, *Chorizagrotis auxiliaris*. *Journal of Agricultural Research. 6*(23): 871–881. https://www.cabidigitallibrary.org/doi/full/10.5555/19160500950

Coop JD, Hibner CD, Miller AJ, et al. 2005. Black bears forage on army cutworm moth aggregations in the Jemez Mountains, New Mexico. *The Southwestern Naturalist. 50*(2): 278–281. https://doi.org/10.1894/0038-4909(2005)050[0278:BBFOAC]2.0.CO;2

Corradini A, Haroldson MA, Cagnacci F, et al. 2023. Evidence for density-dependent effects on body composition of a large omnivore in a changing Greater Yellowstone Ecosystem. *Global Change Biology. 29*(16): 4496–4510. https://doi.org/10.1111/gcb.16759

Crabo LG. 2018. A new genus and three new species of noctuid moths from western United States of America and Mexico (Lepidoptera, Noctuidae, Noctuinae, *Eriopygini*). *ZooKeys. 788*:183–199. https://doi.org/10.3897/zookeys.788.26068

Cristescu B, Stenhouse GB, Boyce MS. 2015. Grizzly bear diet shifting on reclaimed mines. *Global Ecology and Conservation. 4*: 207–220. https://doi.org/10.1016/j.gecco.2015.06.007

Dirnböck T, Essl F, Rabitsch W. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology. 17*(2): 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Dickinson MH, Lehmann FO, Sane SP. 1999. Wing rotation and the aerodynamic basis of insect flight. *Science. 284*(5422): 1954–1960. https://doi.org/10.1126/science.284.5422.1954

Dittemore CM. 2022. Natal Origin, Migratory Patterns, and Abundance of the Army Cutworm, Euxoa auxiliaris. Thesis. Montana State University, Bozeman, Montana. https://scholarworks.montana.edu/items/e08ebc9c-351c-4a11-889a-341e45c88820?show=full

Dittemore CM, Tyers DB, Weaver DK, et al. 2023. Using stable isotopes to determine natal origin and feeding habits of the army cutworm moth, Euxoa auxiliaris (Lepidoptera: Noctuidae). *Environmental Entomology. 52*(2): 230–242. https://doi.org/10.1093/ee/nvad006

Drake VA, Farrow RA. 1988. The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology. 33*(1): 183–210. https://doi.org/10.1146/annurev.en.33.010188.001151

Drake VA, Reynolds DR. 2012. Radar entomology: observing insect flight and migration. *Cabi.*

Drecktrah HG. 1978. Morphology of the internal reproductive system of the adult female army cutworm, *Euxoa auxiliaris*. *Annals of the Entomological Society of America. 71*(6): 923–927. https://doi.org/10.1093/aesa/71.6.923

Drecktrah HG. 1978. Morphology of the internal reproductive system of the adult female army cutworm, *Euxoa auxiliaris*. *Annals of the Entomological Society of America. 71*(6): 923–927. https://doi.org/10.1093/aesa/71.6.923

Dreyer D, El Jundi B, Kishkinev D, et al. 2018. Evidence for a southward autumn migration of nocturnal noctuid moths in central Europe. *Journal of Experimental Biology. 221*(24): jeb179218. https://doi.org/10.1242/jeb.179218

Dreyer D, Frost B, Mouritsen H, et al. 2018. The earth’s magnetic field and visual landmarks steer migratory flight behavior in the nocturnal Australian bogong moth. *Current Biology. 28*(13): 2160–2166.e5. https://doi.org/10.1016/j.cub.2018.05.030

Eberhardt LL. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology. 83*(10): 2841–2854. https://doi.org/10.1890/0012 9658(2002)083[2841:APFPAO]2.0.CO;2

Ellington CP. 1999. The novel aerodynamics of insect flight: Applications to micro-air vehicles. *Journal of Experimental Biology. 202*(23): 3439–3448. https://doi.org/10.1242/jeb.202.23.3439

Ellis S. 2014. Cutworms damage fields in Oregon, Idaho, Sugar Producer Magazine. April 30, 2014. https://www.sugarproducer.com/2014/04/cutworms-damage-fields-in-oregon

Erlenbach JA, Rode KD, Raubenheimer D, et al. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. *Journal of Mammalogy. 95*(1): 160–168. https://doi.org/10.1644/13-MAMM-A-161

Felicetti LA, Robbins CT, Shipley LA. 2003. Dietary protein content alters energy expenditure and composition of the mass gain in grizzly bears (*Ursus arctos horribilis*). *Physiological and Biochemical Zoology*. *76*(2): 256–261 https://doi.org/10.1139/z03-054

Feng H, Wu X, Wu B, et al. 2009. Seasonal migration of *Helicoverpa armigera* (Lepidoptera: Noctuidae) over the Bohai Sea. *Journal of Economic Entomology. 102(*1): 95–104. https://doi.org/10.1603/029.102.0114

Floate KD, Hervet VA. 2017. Noctuid (Lepidoptera: Noctuidae) pests of canola in North America. In Integrated management of insect pests on canola and other Brassica oilseed crops. p. 96–113. Wallingford UK: *CABI*. http://ebookcentral.proquest.com/lib/montana/detail.action?docID=5898008

Fortin JK, Schwartz CC, Gunther KA, et al. 2013. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of wildlife management*. *77*(2): 270–281. https://doi.org/10.1002/jwmg.483

French SP, French MG, Knight RR. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. Bears: *Their Biology and Management. 9*: 389–399. https://doi.org/10.2307/3872725

Gatehouse AG. 1994. Insect migration: variability and success in a capricious environment. *Population Ecology. 36*(2): 165–171. https://doi.org/10.1007/BF02514932

Gatehouse AG. 1997. Behavior and ecological genetics of wind-borne migration by insects. *Annual review of entomology. 42*(1): 475–502. https://doi.org/10.1146/annurev.ento.42.1.475

Gardner CL, Pamperin NJ, Benson JF. 2014. Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. *Ursus. 25*(2): 121–138. https://doi.org/10.2192/URSUS-D-14-00015.1

Gillette CP. 1903. Some of the more important insects of 1903. Bulletin of the Colorado Agriculture Experiment Station. 94.

https://books.google.com/books?hl=en&lr=&id=y4QoAAAAYAAJ&oi=fnd&pg=PA3&dq=Gillette,+C.+P.+1903.+Some+of+the+more+important+insects+of+1903.+Bulletin+of+the+Colorado+Agriculture+Experiment+Station,+94.+&ots=F5tcyjfXbW&sig=iqIemFZRAIDpFWt_MwKehmw-Jrw#v=onepage&q&f=false

Graham K, Stenhouse GB. 2014. Home range, movements, and denning chronology of the grizzly bear (Ursus arctos) in west-central Alberta. *The Canadian Field-Naturalist. 128*(3): 223–234. https://doi.org/10.22621/cfn.v128i3.1600

Grimm NB, Chapin III FS, Bierwagen B, et al. 2013. The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment. 11*(9): 474–482. https://doi.org/10.1890/120282

Gunther KA, Haroldson MA, Frey K, et al. 2004. Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000. *Ursus. 15*(1): 10–22. https://doi.org/10.2192/1537-6176(2004)015%3C0010:GBCITG%3E2.0.CO;2

Gunther KA, Shoemaker RR, Frey KL, et al. 2014. Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus. 25*(1): 60–72. https://doi.org/10.2192/URSUS-D-13-00008.1

Hanski I, Pöyry J. 2007. Insect populations in fragmented habitats. In Stewart AJA, New TR, Lewis OT (Eds.) Insect Conservation Biology: Proceedings of the Royal Entomological Society's 23rd Symposium. *CABI* p. 175–202. https://doi.org/10.1079/9781845932541.0175

Hardwick DF, Lefkovitch LP. 1971. Physical and biotic factors affecting *Euxoa* species abundance in western North America: A regression analysis. *The Canadian Entomologist. 103*(9): 1217–1235. https://doi.org/10.4039/Ent1031217-9

Heinrich B. 1986. Comparative thermoregulation of four montane butterflies of different mass. *Physiological Zoology. 59*(6): 616-626. https://doi.org/10.1086/physzool.59.6.30158609

Heinrich B. 1981. Temperature regulation during locomotion in insects. In Herreid CF, Fourtner CR (Eds.) Locomotion and Energetics in Arthropods Springer. Boston MA. p 391–417. https://doi.org/10.1007/978-1-4684-4064-5_15

Hendrix III W, Mueller T, Phillips J, et al. 1987. Pollen as an indicator of long-distance movement of *Heliothis zea* (Lepidoptera: Noctuidae). *Environmental Entomology. 16*(5): 1148–1151. https://doi.org/10.1093/ee/16.5.1148

Hendrix WH, Showers WB. 1992. Tracing black cutworm and armyworm (Lepidoptera: Noctuidae) northward migration using Pithecellobium and Calliandra pollen. *Environmental Entomology. 21*(5): 1092–1096. https://doi.org/10.1093/ee/21.5.1092

Hilderbrand GV, Jenkins SG, Schwartz CC, et al. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology. 77*(10): 1623–1630. https://doi.org/10.1139/z99-133

Hilty JA, Lidicker Jr WZ, Merenlender AM. 2012. Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island press.

Inouye DW. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*. *89*(2): 353–362. https://doi.org/10.1890/06-2128.1

Hobson KA, Doward K, Kardynal KJ, Mcneil JN. 2018. Inferring origins of migrating insects using isoscapes: A case study using the true armyworm, *Mythimna unipuncta,* in North America. *Ecological Entomology. 43*(3): 332–341. https://doi.org/10.1111/een.12505

Hoffmann AA, Chown SL, Clusella-Trullas S. 2013. Upper thermal limits in terrestrial ectotherms: How constrained are they? *Functional Ecology. 27*(4): 934–949. https://doi.org/10.1111/j.1365-2435.2012.02036.x

Hoffmann AA, Sørensen JG, Loeschcke V. 2003. Adaptation of Drosophila to temperature extremes: Bringing together quantitative and molecular approaches. *Journal of thermal Biology. 28*(3): 175–216. https://doi.org/10.1016/S0306-4565(02)00057-8

Hostetler S, Whitlock C, Shuman B, et al. 2021. Greater Yellowstone climate assessment: Past, present, and future climate change in greater Yellowstone watersheds. Montana State University, Institute on Ecosystems. https://scholarworks.montana.edu/items/f1d98481-7491-4242-b3a6-8899c173b8ef

Inouye DW. 2020. Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences. 1469*(1): 26–37. https://doi.org/10.1111/nyas.14104

Iowa Environmental Mesonet. Iowa State University of Science and Technology. https://mesonet.agron.iastate.edu/

Jacobson LA, Blakeley PE. 1959. Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America. 52*(1): 100–105. https://doi.org/10.1093/aesa/52.1.100

Jiménez-Pérez, A., & Wang, Q. (2004). Effect of body weight on reproductive performance in *Cnephasia jactatana* (Lepidoptera: Tortricidae). *Journal of Insect Behavior. 17*: 511–522.

Johnson SJ. 1987. Migration and the life history strategy of the fall armyworm, Spodoptera frugiperda in the western hemisphere. *International Journal of Tropical Insect Science. 8*(4-5-6): 543–549. https://doi.org/10.1017/S1742758400022591

Jones HW, Byers JR, Butts RA, et al. 1990. Insects and related pests of cereal crops –Alberta. *The Canadian Agricultural Insect Pest Review. 68:* 13–14.

Käfer H, Kovac H, Simov N, et al. 2020. Temperature tolerance and thermal environment of European seed bugs. *Insects. 11*(3): 197. https://doi.org/10.3390/insects11030197

Kammer AE. 1970. Thoracic temperature, shivering, and flight in the monarch butterfly, Danaus plexippus (L.). *Zeitschrift für vergleichende Physiologie. 68*(3): 334–344.

Keiter RB. 1989. Taking account of the ecosystem on the public domain: law and ecology in the Greater Yellowstone region. *U. Colo. L. Rev. 60*: 923. http://dx.doi.org/10.2139/ssrn.3534327

Kellermann V, van Heerwaarden B. 2019. Terrestrial insects and climate change: Adaptive responses in key traits. *Physiological Entomology. 44*(2): 99–115.

Kendall DM, Kevan PG, LaFontaine JD. 1981. Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist. 113*(7): 607–614. https://doi.org/10.4039/Ent113607-7

Kennedy TE, Sing SE, Peterson RK. 2025. Critical thermal limits of the seasonal migrant, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). *Environmental Entomology*. nvaf019. https://doi.org/10.1093/ee/nvaf019

Keosentse O, Mutamiswa R, Du Plessis H, et al. 2021. Developmental stage variation in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) low temperature tolerance: Implications for overwintering. *Austral Entomology. 60*(2): 400–410. https://doi.org/10.1111/aen.12536

Kevan PG, Kendall DM. 1997. Liquid assets for fat bankers: Summer nectarivory by migratory moths in the Rocky Mountains, Colorado, USA. *Arctic and Alpine Research. 29*(4): 478–482. https://doi.org/10.1080/00040851.1997.12003268

Klok CJ, Chown SL. 1997. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* (Lepidoptera: Tineidae). *Journal of Insect Physiology. 43*(7): 685-694.

Koel TM, Bigelow PE, Doepke PD, et al. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries. 30*(11): 10–19. https://doi.org/10.1577/1548-8446(2005)30[10:NLTRIY]2.0.CO;2

Koerwitz F, Pruess K. 1964. Migratory potential of the army cutworm. *Journal of the Kansas Entomological Society. 37*(3): 234–239. https://www.jstor.org/stable/25083389

Kudo G. 2016. Landscape structure of flowering phenology in alpine ecosystems: significance of plant–pollinator interactions and evolutionary aspects. *Structure and function of mountain ecosystems in Japan: Biodiversity and vulnerability to climate change*. p. 41–62. https://doi.org/10.1007/978-4-431-55954-23

Lapshin DN, Vorontsov DD. 2007. Acoustic irradiation produced by flying moths (Lepidoptera, Noctuidae). *Entomological Review. 87*(9): 1115–1125. https://doi.org/10.1134/S0013873807090035

Lark TJ, Spawn SA, Bougie M, et al. 2020. Cropland expansion in the United States produces marginal yields at high costs to wildlife. *Nature Communications. 11*(1):4295. https://doi.org/10.1038/s41467-020-18045-z

Larson ER, Kipfmueller KF. 2012. Ecological disaster or the limits of observation? Reconciling modern declines with the long-term dynamics of whitebark pine communities. *Geography Compass. 6*(4): 189–214. https://doi.org/10.1111/j.1749-8198.2012.00481.x

Léger A, Cormier SB, Blanchard A, et al. 2024. Investigating the thermal sensitivity of key enzymes involved in the energetic metabolism of three insect species. *Journal of Experimental Biology. 227*(10) https://doi.org/10.1242/jeb.247221

Lemière L, Thiel A, Fuchs B, et al. 2022. Extrinsic and intrinsic factors drive the timing of gestation and reproductive success of Scandinavian brown bears. *Frontiers in Ecology and Evolution. 10*: 1045331. https://doi.org/10.3389/fevo.2022.1045331

Li X, Zhou Y, Wu K. 2023. Biological characteristics and energy metabolism of migrating insects. *Metabolites. 13*(3): 439. https://doi.org/10.3390/metabo13030439

Lobell DB, Hicke JA, Asner GP, et al. 2002. Satellite estimates of productivity and light use efficiency in United States agriculture, 1982–98. *Global Change Biology. 8*(8): 722–735. https://doi.org/10.1046/j.1365-2486.2002.00503.x

Loeschcke V, Hoffmann AA. 2007. Consequences of heat hardening on a field fitness component in Drosophila depend on environmental temperature. *The American Naturalist. 169*(2): 175–183. https://doi.org/10.1086/510632

López-Alfaro C, Robbins CT, Zedrosser A, et al. 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecological Modelling. 270*: 1–10. https://doi.org/10.1016/j.ecolmodel.2013.09.002

López-Alfaro C, Coogan SC, Robbins CT, et al. 2015. Assessing nutritional parameters of brown bear diets among ecosystems gives insight into differences among populations. *PLoS One. 10*(6): e0128088.https://doi.org/10.1371/journal.pone.0128088

Lozano KN. 2022. Food resources for grizzly bears at army cutworm moth aggregation sites in the Greater Yellowstone Ecosystem. Master's Thesis. Montana State University, Bozeman, Montana. https://scholarworks.montana.edu/xmlui/bitstream/handle/1/16932/lozano-food-resources-2022.pdf?sequence=3

Mace RD, Waller JS. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *The Journal of Wildlife Management*. 39–52. https://www.jstor.org/stable/3802412

MacMillan HA, Williams CM, Staples JF, et al. 2012. Metabolism and energy supply below the critical thermal minimum of a chill-susceptible insect. *Journal of Experimental Biology. 215*(8): 1366–1372. https://doi.org/10.1242/jeb.066381

Manglitz GR, Schalk JM, Andersen LW, et al. 1973. Control of the army cutworm on alfalfa in Nebraska. *Journal of Economic Entomology. 66*(1): 299–299. https://doi.org/10.1093/jee/66.1.299

Masters AR, Malcolm SB, Brower LP. 1988. Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. *Ecology. 69*(2): 458–467.

Mattson DJ, Reid MM. 1991a. Conservation of the Yellowstone grizzly bear. *Conservation Biology*. *5*(3): 364–372. https://doi.org/10.1111/j.1523-1739.1991.tb00150.x

Mattson DJ, Gillin CM, Benson SA, et al. 1991b. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology. 69*(9): 2430–2435. https://doi.org/10.1139/z91-341

Mattson DJ, Herrero S, Wright RG, Pease CM. 1996. Science and management of Rocky Mountain grizzly bears. *Conservation biology*. *10*(4): 1013–1025. https://doi.org/10.1046/j.1523-1739.1996.10041013.x

Mattson DJ. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation*. *81*(1-2): 161–177. https://doi.org/10.1016/S0006-3207(96)00142-5

Mbande A, Mutamiswa R, Chidawanyika F. 2023. Thermal tolerance in *Spodoptera frugiperda*: Influence of age, sex, and mating status. *Scientific African. 22*, e01911. https://doi.org/10.1016/j.sciaf.2023.e01911

McHugh ML. 2011. Multiple comparison analysis testing in ANOVA. *Biochemia Medica. 21*(3): 203–209.

Merlin C, Heinze S, Reppert SM. 2012. Unraveling navigational strategies in migratory insects. *Current opinion in neurobiology. 22*(2): 353–361. https://doi.org/10.1016/j.conb.2011.11.009

Michaud JP, Martin TJ, Jyoti JL. 2006. Larval preference for a wheat cultivar in the army cutworm (Lepidoptera: Noctuidae). *Journal of the Kansas Entomological Society. 79*(1): 28–33. https://doi.org/10.2317/0022-8567(2006)079[0028:LPFAWC]2.0.CO;2

Middleton AD, Morrison TA, Fortin JK, et al. 2013. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences*. *280*(1762): 20130870. https://doi.org/10.1098/rspb.2013.0870

Mock CJ. 1996. Climatic controls and spatial variations of precipitation in the western United States. *Journal of Climate*. *9*(5): 1111–1125. https://doi.org/10.1175/1520-0442(1996)009%3C1111:CCASVO%3E2.0.CO;2

Munson SM, Sher AA. 2015. Long-term shifts in the phenology of rare and endemic Rocky Mountain plants. *American journal of botany*. *102*(8): 1268–1276. https://doi.org/10.3732/ajb.1500156

Mutamiswa R, Chidawanyika F, Nyamukondiwa C. 2017. Dominance of spotted stemborer *Chilo partellus Swinhoe* (Lepidoptera: Crambidae) over indigenous stemborer species in Africa's changing climates: ecological and thermal biology perspectives. *Agricultural and Forest Entomology. 19*(4): 344–356. https://doi.org/10.1111/afe.12217

Mutamiswa R, Mbande A, Nyamukondiwa C, et al. 2023. Thermal adaptation in Lepidoptera under shifting environments: Mechanisms, patterns, and consequences. *Phytoparasitica. 51*(5): 929–955. https://doi.org/10.1007/s12600-023-01095-6

Nelson RA, Folk Jr GE, Pfeiffer EW, et al. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: their biology and management*. p. 284–290. https://www.jstor.org/stable/3872551

Neven LG. 2000. Physiological responses of insects to heat. *Postharvest Biology Technology. 21*(1): 103–111. https://doi.org/10.1016/S0925-5214(00)00169-1

Neuvonen S, Virtanen T. 2015. Abiotic factors, climatic variability and forest insect pests. In Climate change and insect pests. (pp. 154-172). Wallingford UK: CABI.

Nielsen SE, Cattet MR, Boulanger J, et al. 2013. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. BMC ecology. 13: 1–13. https://doi.org/10.1186/1472-6785-13-31

Nilsson C, Grelsson G. 1995. The fragility of ecosystems: a review. *Journal of Applied Ecology*. p. 677–692. https://doi.org/10.2307/2404808

Noss RF, Carroll C, Vance-Borland K, Wuerthner G. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology. 16*(4): 895–908. https://doi.org/10.1046/j.1523-1739.2002.01405.x

Nunlist EA, Tyers D, Pils A, et al. 2023. Grizzly bears and humans at alpine moth sites in Wyoming, USA. *Human-Wildlife Interactions. 17*(1): 71–85. https://www.jstor.org/stable/27316539

Nunlist E. A. 2020. Grizzly bears and humans at two moth aggregation sites in Wyoming. Thesis. Montana State University. Bozeman, Montana. https://scholarworks.montana.edu/items/a931b40e-9183-4075-8000-17409fae0376

O'Brien SL, Lindzey F. 1994. Grizzly bear use of moth aggregation sites and summer ecology of army cutworm moths in the Absaroka Mountains, Wyoming. Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming. https://search.worldcat.org/it/title/Grizzly-bear-use-of-moth-aggregation-sites-and-summer-ecology-of-army-cutworm-moths-in-the-Absaroka-Mountains-Wyoming-:-final-report/oclc/48960914

O’Brien SL, Lindzey FG. 1998. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus. 10*:427–435. https://www.jstor.org/stable/3873154

Oregon State University. 2024. PRISM Climate Group, Oregon State University. https://prism.oregonstate.edu/explorer/

Palomo I. 2017. Climate change impacts on ecosystem services in high mountain areas: a literature review. *Mountain Research and Development. 37*(2): 179–187. https://doi.org/10.1659/MRD-JOURNAL-D-16-00110.1

Parmesan C, Ryrholm N, Stefanescu C, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature. 399*(6736): 579–583.

Pease CM, Mattson DJ. 1999. Demography of the Yellowstone grizzly bears. *Ecology. 80*(3): 957–975. https://doi.org/10.1890/0012-9658(1999)080[0957:DOTYGB]2.0.CO;2

Pederson GT, Gray ST, Woodhouse CA, et al. 2011. The unusual nature of recent snowpack declines in the North American Cordillera. *Science. 333*(6040): 332–335. https://doi.org/10.1126/science.1201570

Pepper J. 1932. Observations on a unidirectional flight of army cutworm moths and their possible bearing on aestivation. *The Canadian Entomologist. 64*(11): 241–242. https://doi.org/10.4039/Ent64241-11

Phillips MK. 1987. Behavior and habitat use of grizzly bears in northeastern Alaska. Bears: Their Biology and Management. 159–167. https://www.jstor.org/stable/3872622

Pierce KL, Despain DG, Morgan LA, Good JM. 2007. The Yellowstone hotspot, greater Yellowstone ecosystem, and human geography. https://digitalcommons.unl.edu/usgspubs/79/

Pigeon KE, Stenhouse G, Côté SD. 2016. Drivers of hibernation: linking food and weather to denning behaviour of grizzly bears. *Behavioral Ecology and Sociobiology. 70*:1745–1754. https://doi.org/10.1007/s00265-016-2180-5

Piyaphongkul J, Pritchard J, Bale J. 2014. Effects of acclimation on the thermal tolerance of the brown planthopper Nilaparvata lugens (S tål). *Agricultural and Forest Entomology. 16*(2): 174–183. https://doi.org/10.1111/afe.12047

Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual review of ecology and systematics. 28*(1): 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

Pruess KP. 1961. Distribution of army cutworm larvae in wheat and barley fields. *Journal of Economic Entomology. 54*(2): 250–252. https://doi.org/10.1093/jee/54.2.250

Pruess, K. P. 1963. Effects of food, temperature, and oviposition site on longevity and fecundity of the army cutworm, *Chorizagrotis Auxiliaris. Journal of Economic Entomology. 56*(2), 219–221. https://academic.oup.com/jee/article/56/2/219/2207489

Pruess KP. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaries* (Lepidoptera: Noctuidae). I. Evidence for a migration. *Annals of the Entomological Society of America*. *60*(5): 910–920. https://doi.org/10.1093/aesa/60.5.910

Pruess KP, Pruess NC. 1971. Telescopic observation of the moon as a means for observing migration of the army cutworm, *Chorizagrotis Auxiliaris* (Lepidoptera: Noctuidae). *Ecology*. *52*(6): 999–1007. https://doi.org/10.2307/1933805

Qi G-J, Ma J, Wan J, et al. 2021. Source regions of the first immigration of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) invading Australia. *Insects. 12*(12) https://doi.org/10.3390/insects12121104

Rainey RC. 1967. Radar observations of locust swarms. *Science. 157*(3784): 98–99. https://doi.org/10.1126/science.157.3784.98

Ramos-Jiliberto R, Domínguez D, Espinoza C, et al. 2010. Topological change of Andean plant–pollinator networks along an altitudinal gradient. *Ecological Complexity. 7*(1): 86–90. https://doi.org/10.1016/j.ecocom.2009.06.001

Ramos-Jiliberto R, Moisset de Espanés P, Vázquez DP. 2020. Pollinator declines and the stability of plant–pollinator networks. *Ecosphere. 11*(4): e03069. https://doi.org/10.1002/ecs2.3069

Rankin MA, McAnelly ML, Bodenhamer JE. 1986. The oogenesis-flight syndrome revisited. In *Insect flight: dispersal and migration*. p. 27–48. Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-71155-8_3

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved November 22, 2024 from https://www.Rproject.org/

Régnière J, Garcia M, Saint-Amant R. 2019. Modeling migratory flight in the spruce budworm: Circadian rhythm. *Forests. 10*(10): 877. https://doi.org/10.3390/f10100877

Régnière J, Delisle J, Sturtevant BR, et al. 2019. Modeling migratory flight in the spruce budworm: Temperature constraints. *Forests. 10*(9): 802. https://doi.org/10.3390/f10090802

Reynolds DR, Chapman JW, Drake VA. 2017. Riders on the wind: The aeroecology of insect migrants. In Chilson PB, Frick WF, Kelly JF, et al. (Eds.) *Aeroecology.* p 145–178. Springer. https://doi.org/10.1007/978-3-319-68576-2_7

Reynolds AM, Reynolds DR, Sane SP, et al. 2016. Orientation in high-flying migrant insects in relation to flows: mechanisms and strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences. 371*(1704): 20150392. https://doi.org/10.1098/rstb.2015.0392

Riley JR, Reynolds DR, Smith AD, et al. 1995. Observations of the autumn migration of the rice leaf roller Cnaphalocrocis medinalis (Lepidoptera: Pyralidae) and other moths in eastern China. *Bulletin of Entomological Research. 85*(3): 397–414. https://doi.org/10.1017/S0007485300036130

Robbins CT, Ben-David M, Fortin JK, et al. 2012. Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy. 93*(2): 540–546. https://doi.org/10.1644/11-MAMM-A-155.1

Robison HL, Schwartz CC, Petty JD, et al. 2006. Assessment of pesticide residues in army cutworm moths (Euxoa auxiliaris) from the Greater Yellowstone Ecosystem and their potential consequences to foraging grizzly bears (*Ursus arctos horribilis*). *Chemosphere. 64*(10): 1704–1712. https://doi.org/10.1016/j.chemosphere.2006.01.006

Robison HL. 2009. Relationships between Army Cutworm Moths and Grizzly Bear Conservation. Thesis. University of Nevada, Reno, Nevada. https://scholarwolf.unr.edu/items/e79fffbe-49b1-4762-be75-bb2194008c0b

Saura S, Bastin L, Battistella L, et al. 2017. Protected areas in the world's ecoregions: How well connected are they?. *Ecological Indicators. 76*: 144–158. https://doi.org/10.1016/j.ecolind.2016.12.047

Schmaljohann H, Liechti F, Bächler E, et al. 2008. Quantification of bird migration by radar–a detection probability problem. *Ibis. 150*(2): 342–355. https://doi.org/10.1111/j.1474-919X.2007.00797.x

Schwartz CC, Miller SD, Haroldson MA. 2003. Grizzly bear. *Wild mammals of North America: biology, management, and conservation. 2*: 556–586. https://www.researchgate.net/profile/Sterling-Miller/publication/313220567_Grizzly_bear_Ursus_arctos/links/5898e579a6fdcc32dbdd0b28/Grizzly-bear-Ursus-arctos.pdf

Schwartz CC, Haroldson MA, White GC. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *The Journal of Wildlife Management. 74*(4): 654–667. https://doi.org/10.2193/2009-206

Schwartz CC, Fortin JK, Teisberg JE, et al. 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *The Journal of wildlife management. 78*(1): 68–78. https://doi.org/10.1002/jwmg.633

Seastedt TR, Oldfather MF. 2021. Climate change, ecosystem processes and biological diversity responses in high elevation communities. *Climate. 9*(5): 87. https://doi.org/10.3390/cli9050087

Servheen C. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *The Journal of Wildlife Management*. p. 1026–1035. https://www.jstor.org/stable/3808161

Sgrò CM, Terblanche JS, Hoffmann AA. 2016. What can plasticity contribute to insect responses to climate change? *Annual Review of Entomology. 61*: 433–451.

Shah AA, Woods HA, Havird JC, et al. 2021. Temperature dependence of metabolic rate in tropical and temperate aquatic insects: Support for the climate variability hypothesis in mayflies but not stoneflies. *Global Change Biology. 27*(2): 297–311. https://doi.org/10.1111/gcb.15400

Shinker JJ. 2010. Visualizing spatial heterogeneity of western US climate variability. *Earth Interactions. 14*(10): 1–15. https://doi.org/10.1175/2010EI323.1

Showers WB, Whitford F, Smelser RB, et al. 1989. Direct evidence for meteorologically driven long-range dispersal of an economically important moth. *Ecology. 70*: 987–992. https://doi.org/10.2307/1941366

Smith AP, Sundstrom A, Burnham M. 2024. Understanding diverse perspectives on grizzly–livestock conflict and conflict-reduction tools across southwest Montana ranching communities. *The Journal of Wildlife Management*. *89*(3). e22709. https://doi.org/10.1002/jwmg.22709

Snow SJ. 1925. Observations on the cutworm, *Euxoa auxiliaris* Grote, and its principal parasites. *Journal of Economic Entomology. 18*(4): 602–609. https://doi.org/10.1093/jee/18.4.602

Sørensen JG, Kristensen, TN, Loeschcke V., et al. 2015. No trade-off between high and low temperature tolerance in a winter acclimatized Danish *Drosophila subobscura* population. *Journal of Insect Physiology. 77*: 9–14.

Soteres KM, Berberet RC, and McNew RW. 1984. Parasites of larval *Euxoa auxiliaris* (Groté) and Peridroma saucia (Hübner) (Lepidoptera: Noctuidae) in Alfalfa Fields of Oklahoma. *Journal of the Kansas Entomological Society. 57*(1): 63–68.

Srygley RB, Dudley R, Hernandez EJ, et al. 2023. Quantifying the aerodynamic power required for flight and testing for adaptive wind drift in passion-vine butterflies *Heliconius sara* (Lepidoptera: Nymphalidae). *Insects. 14*(2):112. https://doi.org/10.3390/insects14020112

Stange EE, Ayres MP. 2010. Climate change impacts: Insects. *Encyclopedia of life sciences*. 1. https://doi.org/10.1002/9780470015902.a0022555

Steenweg R, Hebblewhite M, Burton C, et al. 2023. Testing umbrella species and food-web properties of large carnivores in the Rocky Mountains. *Biological Conservation. 278*: 109888. https://doi.org/10.1016/j.biocon.2022.109888

Stevenson RD, Josephson RK. 1990. Effects of operating frequency and temperature on mechanical power output from moth flight muscle. *Journal of Experimental Biology. 149*(1): 61–78. https://doi.org/10.1242/jeb.149.1.61

Strickland EH. 1916. The army cutworm: *Euxoa* (*Chorizagrotis*) *auxiliaris* Grote. *Canadian Department of Agricultural Entomology*. (Bulletin No. 13). https://www.canadiana.ca/view/oocihm.83630/1

Sunday JM, Bates AE, Kearney MR, et al. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences. 111*(15): 5610–5615. https://doi.org/10.1073/pnas.1316145111

Swanson CS, McCollum DW, Maj M. 1994. Insights into the economic value of grizzly bears in the Yellowstone recovery zone. *Bears: Their Biology and Management*. p. 575–582. https://doi.org/10.2307/3872746

Syskine DV, Boggs CL. 2025. Flying by night: Comparing nocturnal pollinator networks over time in the Colorado Rocky Mountains. *Ecological Entomology. 50*(2): 235–246. https://doi.org/10.1111/een.13399

Taylor LR, Carter CI. 1961. The analysis of numbers and distribution in an aerial population of Macrolepidoptera. *Transactions of the Royal Entomological Society of London. 113*(12):369–386. https://doi.org/10.1111/j.1365-2311.1961.tb02296.x

Taylor GK. 2001. Mechanics and aerodynamics of insect flight control. *Biological Reviews. 76*(4): 449–471. https://doi.org/10.1017/S1464793101005759

Templeton AR, Robertson RJ, Brisson J, et al. 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Sciences of the United States of America. 98*(10): 5426–5432. https://doi.org/10.1073/pnas.091093098

Terblanche JS, Hoffmann AA, Mitchell KA, et al. 2011. Ecologically relevant measures of tolerance to potentially lethal temperatures. *Journal of Experimental Biology. 214*(22): 3713–3725. https://doi.org/10.1242/jeb.061283

Tercek M, Rodman A, Thoma D. 2015. Trends in Yellowstone snowpack. *Yellowstone Science. 23*(1): 20–27. https://www.researchgate.net/profile/Tony-Chang-10/publication/275345000_Historic_and_Projected_Climate_Change_in_the_Greater_Yellowstone_Ecosystem/links/55394e500cf247b858812ab2/Historic-and-Projected-Climate-Change-in-the-Greater-Yellowstone-Ecosystem.pdf#page=20

Thornton PK, Ericksen PJ, Herrero M, et al. 2014. Climate variability and vulnerability to climate change: A review. *Global Change Biology. 20*(11): 3313–3328. https://doi.org/10.1111/gcb.12581

Toolson EC., & Hadley NF. 1974. Thermal tolerance of beet armyworm moths, *Spodoptera exigua*: Effects of age, temperature acclimation, and gamma radiation. *Environmental Entomology. 3*(2): 290–294. https://doi.org/10.1093/ee/3.2.290

U.S. Geological Survey. (2016, April 6). Graph: Average temperature at Alpine weather station in Glacier NP. U.S. Department of the Interior. https://www.usgs.gov/media/images/graph-average-temperature-alpine-weather-station-glacier-np

Walkden HH. 1950. Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains. *U.S. Dept. of Agriculture. 849*:19–21. Retrieved September 05, 2024 from https://www.biodiversitylibrary.org/item/130872

Walters CK, Winkler JA, Shadbolt RP, et al. 2008. A long-term climatology of southerly and northerly low-level jets for the Central United States. *Annals of the Association of American Geographers. 98*(3): 521–552. https://doi.org/10.1080/00045600802046387

Watson JE, Iwamura T, Butt N. 2013. Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Climate Change. 3*(11): 989–994. https://doi.org/10.1038/nclimate2007

Wells SL, McNew LB, Tyers DB, et al. 2019. Grizzly bear depredation on grazing allotments in the Yellowstone Ecosystem. *The Journal of Wildlife Management. 83*(3): 556–566. https://doi.org/10.1002/jwmg.21618

West JB. 1996. Prediction of barometric pressures at high altitudes with the use of model atmospheres. *Journal of Applied Physiology. 81*(4):1850–1854. https://doi.org/10.1152/jappl.1996.81.4.1850

Westbrook JK. 2008. Noctuid migration in Texas within the nocturnal aeroecological boundary layer. *Integrative and Comparative Biology. 48*(1): 99–106. https://doi.org/10.1093/icb/icn040

Whipple S, Bowser G. 2023. The buzz around biodiversity decline: Detecting pollinator shifts using a systematic review. *Iscience. 26*(11). https://doi.org/10.1016/j.isci.2023.108101

White Jr D, Kendall KC, Picton HD. 1998a. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology. 76*(2): 221–227. https://doi.org/10.1139/z97-185

White D, Kendall KC, Picton HD. 1998b. Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology. 76*(5): 835–842. https://doi.org/10.1139/z98-001

White Jr D, Kendall KC, Picton HD. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildlife Society Bulletin*. 146–151. https://www.jstor.org/stable/3783951

White PJ, Gunther KA, Van Manen FT, et al. 2017. Yellowstone grizzly bears: ecology and conservation of an icon of wildness. (*No Title*). https://www.researchgate.net/publication/318324730_Yellowstone_Grizzly_Bears_Ecology_and_Conservation_of_an_Icon_of_Wildness

Wielgus RB, Sarrazin F, Ferriere R, Clobert J. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation. 98*(3): 293–303. https://doi.org/10.1016/S0006-3207(00)00168-3

Wilcox EV. 1898. The grain aphis. An army cut-worm. Montana Agricultural Experiment Station, (Bulletin No. 17). https://catalog.hathitrust.org/Record/011481195

Wood CR, Chapman JW, Reynolds DR, et al. 2006. The influence of the atmospheric boundary layer on nocturnal layers of noctuids and other moths migrating over southern Britain. *International Journal of Biometeorology. 50*(4): 193–204. https://doi.org/10.1007/s00484-005-0014-7

Worthen WB, Haney DC. 1999. Temperature tolerance in three *mycophagous* Drosophila species: Relationships with community structure. *Oikos. 86*(1): 113–118. https://doi.org/10.2307/3546575

Xing K, Zhao F. 2022. Acclimation effects of natural daily temperature variation on longevity, fecundity, and thermal tolerance of the diamondback moth (*Plutella xylostella*). *Insects. 13*(4): 309. https://doi.org/10.3390/insects13040309

Xu RB, Ge SS, Yu WH, et al. 2022. Physiological and environmental influences on wingbeat frequency of Oriental Armyworm, *Mythimna separata* (Lepidoptera: Noctuidae). *Environmental Entomology. 52*(1):1–8. https://doi.org/10.1093/ee/nvac101

Young BF, Ruff RL.1982. Population-dynamics and movements of black bears in east central Alberta. *Journal of Wildlife Management 46*: 845–860. https://www.jstor.org/stable/3808217

Yu W, Zhou Y, Guo J, et al. 2020. Interspecific and seasonal variation in wingbeat frequency among migratory Lepidoptera in Northern China. *Journal of Economic Entomology. 113*(5): 2134–2140. https://doi.org/10.1093/jee/toaa134