NATAL ORIGIN, MIGRATORY PATTERNS, AND ABUNDANCE OF THE ARMY CUTWORM MOTH, *EUXOA AUXILIARIS*

by

Clare Mikaela Dittemore

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

of

Master of Science

in

Land Resources and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2022

DEDICATION

I dedicate this thesis to my grandmother, Dr. Kathryn Boyle.

ACKNOWLEDGMENTS

Thank you to my advisor, Dr. Robert K.D. Peterson, for your wonderful sense of humor, encouragement, and seemingly infinite knowledge of insect ecology. Thank you to Dr. Daniel Tyers, my co-advisor, for the field support, stories and poetry, the best chili I have ever had, and organizing the logistics necessary for the completion of this project. Thank you to my committee member, Dr. David Weaver, for your statistical knowledge, innovation, and intelligence. A special thanks to the field crew: Dani Mee, Denali Smith, Heather Brown, Katie Desler,q Katie Gerlach, Oscar Dalling, and Rachael Dines; each of you were integral in the completion of this project. Thank you to the past and present students of the CoBRA Lab: Katerina Lozano, Miles Maxcer, John Bowley, and Benjamin Schwartz. I so appreciate all of you making the CoBRA Lab feel like home and for the support each of you have provided for me. Thank you to Dr. Robert Diehl, for your boundless energy, technical support, and academic advice. Thank you to Dr. Gabriel Bowen, for your stable isotopic wisdom. Thank you to each of our wonderful army cutworm moth collectors in the Great Plains. A special thanks to Dick and Mary Ohman and Gerry Bennett for critical financial support. Thank you to Peter McDonald, Lisa Timchak, Andy Pils, Casey McQuiston, and Kerry Murphy for indispensable support within the Forest Service. Thanks also to the staff on the SNF for logistical assistance, especially with horse trips onto the peaks. This includes Jason Pindell, Jason Brengle, Crosby Davidson, and Jestyn Hicks. I am also grateful to the Greater Yellowstone Coordinating Committee for financial help through several grants. Thank you to Dr. Jennifer Fortin-Noreus and Dr. Hillary Robison for the valuable advice on moth ecology, moth collection, and isotopic analysis. And last but certainly not least, thank you to my family for your support and encouragement in everything I do.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

Figure Page

LIST OF FIGURES CONTINUED

Figure Page

ABSTRACT

The army cutworm moth, *Euxoa auxiliaris*, is a migratory noctuid that migrates from and returns to the Great Plains. At their Rocky Mountain summering range, it is an important food for the Greater Yellowstone Ecosystem (GYE) grizzly bears, *Ursus arctos horribilis*. However, a limited understanding of moth migratory patterns, abundance at summering ranges, and the associated vulnerability and variability of these populations, is a shortfall in agency grizzly bear conservation strategies. Therefore, the objectives of our study were to assess the natal origin of moths collected from two mountain ranges and within the Great Plains, characterize larval feeding habits of migrants collected from the Absaroka Range, and assess a monitoring protocol to determine moth abundance at a GYE aggregation site. Using stable isotopes, we estimated the natal origin of migrants collected from the Absaroka and Lewis Ranges, examined migratory patterns within the Great Plains, and assessed the larval feeding habits of migrants collected in the Absaroka Range during 2017-2021. To estimate abundance, we sampled the airspace with a radar stationed within 1 km of an aggregation site in the GYE during 2020 and 2021. There was strong evidence that moths collected in the Great Plains and both mountain ranges were migrating north-south, in addition to previously established east-west movement. Although their origins were varied, moths of the Absaroka Range had the highest probability of origin in Alberta and British Columbia, and moderate probability in Montana, Idaho, and Wyoming across all collection years. Lewis Range moths had the highest probability of origin almost exclusively within the lower third of Canada. As larvae, the moths collected from the Absaroka Range fed almost exclusively on C3 plants. We estimate that 5 million moths passed through our radar's sampling plane (160-750 m above ground level and 2600 m across) over the course of 20 hours (5 nights of movement). Overall, our findings suggest that army cutworm moths at aggregation sites are "supplied" by various source locations, and thus insulated against regional declines within their natal origins. Radar should be used at moth aggregation sites to continue monitoring army cutworm moths.

CHAPTER ONE

LITERATURE REVIEW

Introduction

The army cutworm moth, *Euxoa auxiliaris* (Grote; Lepidoptera: Noctuidae), is a migratory noctuid with the unusual status of being of both agricultural and conservational significance (Pruess & Pruess, 1967; Robison et al., 2006; Strickland, 1916). Its common name reflects its role as an agricultural pest—a generalist cutworm that feeds on a wide range of cultivated plant and weed species, marching en masse to the adjacent field after running out of food in the area where it started feeding (Burton et al., 1980). After emerging as an adult, these moths migrate to the Rocky Mountains where they feed on alpine flowers primarily during the night and roost in interstitial talus during the day (Burton et al., 1980; French et al., 1994; Walkden, 1950; White et al., 1998b). Here, these annual aggregations of the moth are an important food source for the grizzly bear (*Ursus arctos horribilis*) because the moth is one of the most calorically dense food items in the Greater Yellowstone Ecosystem (GYE) (French et al., 1994).

Although this moth is an important food source for the grizzly bear, many components of the moth's ecology remain unknown, including the natal origin of the moth as it pertains to its destination in the Rocky Mountains, how they migrate to and from the Rocky Mountains, and the abundance of the moth after reaching the Rocky Mountains (and subsequently the amount of food that is available for the bear). It is therefore important to understand the ecology of this moth to better inform the long-term potential of this insect as a food source for bears, and thus to inform conservational practices for the bear. This review serves to illustrate the work that was done on the army cutworm moth and explore the areas in which our understanding is lacking.

Army cutworm moths

Life cycle

During late summer, adult females will begin to sexually mature and some will mate in the alpine environments (Kevan & Kendall, 1997; Robison et al., 2006). Adults then migrate and return to the Great Plains, where they continue to mate, and females lay as many as 3,000 eggs per individual in the soil near host plants (Figure 1; Figure 2) (Burton et al., 1980; Cooley, 1916a; Johnson, 1905; Kendall, 1981; Strickland, 1916). After oviposition, the adults die (Burton et al., 1980). Larvae emerge in mid-autumn and mature to the first or second instar, overwintering in the soil. In the spring, hibernating larvae emerge to feed on alfalfa or small grains. The larval stage of this insect produces the economic damage when populations are sufficiently large (Burton et al., 1980; Morrill, 1991).

After reaching the sixth or seventh instar, larvae burrow into the soil and form a cell horizontal with the soil surface to pupate (Burton et al., 1980; Seamans, 1928a). Sufficient moisture during the late summer and early autumn is crucial for eggs to hatch (Burton et al., 1980; Seamans, 1928a). After egg hatch, moisture is also critical in fall and spring (Burton et al., 1980). With too much moisture, the larvae may drown or be forced to the surface where they will not have protection from predators. With too little moisture, the larvae may desiccate (Beirne, 1970; Blodgett, 1997). The timing of precipitation and temperature is also critical (Hardwick & Lefkovitch, 1971). As with other insects, predators, parasites, and diseases may also play important roles in the population dynamics of this insect (Johnson, 1905; Snow, 1925; Strickland, 1916; Walkden, 1942).

Shortly after emerging in the spring and early summer, adults migrate to the Rocky Mountains where they increase their lipid stores by feeding on alpine blooms (Kevan & Kendall, 1997; Pruess & Pruess, 1967). During the day, moths hide under the talus, taking advantage of the thermal gradient present to thermoregulate as daily temperatures fluctuate (French et al., 1994; White et al., 1998a). Toward the end of the summer, nocturnal moth activity begins to decline as alpine flowers desiccate and go to seed, and moths migrate back to the plains (French et al., 1994).

Low elevation ecology

The army cutworm moth is an infrequent pest throughout the Great Plains and the interior prairies of Canada (Jacobson & Blakeley, 1959), and outbreaks usually do not occur in successive years (Strickland, 1916; Walkden, 1950). Larvae are known for their generalist feeding habits, and both feeding and observational studies illustrated that the cutworm would feed upon most any plant that was offered, including (but not limited to) wheat, alfalfa, barley, oat, and corn (Cooley, 1910; Strickland, 1916). A complete list of host plants can be found in Burton et al. (1980). In outbreak years, larval density in the field can reach as many as 1,500 larvae/m^2 (Strickland, 1916). Outbreaks are generally preceded by one to two years of average abundance (Burton et al., 1980), while the severity and frequency of outbreaks have oscillated throughout the decades. In the 1950s, outbreaks occurred frequently in Montana, Wyoming, Colorado, Alberta, and Saskatchewan (Jacobson & Blakeley, 1959). In the 1970s, outbreaks also occurred frequently throughout the Great Plains, with an estimated 2,500,000 acres of agricultural land being treated for army cutworm in Oklahoma for one year (USDA, 1951-1975).

In the early 2000s, army cutworm moths were sufficiently numerous to warrant a monitoring program in the Intermountain West of the USA (using pheromone traps) (Blodgett et al., 2003). Efforts were renewed in 2013, in which army cutworm moths were again captured with pheromone traps throughout a monitoring network in Montana. Similarly, in Nevada, outbreaks occur infrequently, and army cutworm larvae can be found regularly in agricultural fields (Jeffrey Knight, personal communication, February 19, 2020). Blacklight trap programs in Nebraska indicate that army cutworm moths are almost never the most species-rich moth collected, but they have been collected in low numbers almost every year since 2009 (University of Nebraska, 2020).

Given that outbreaks of army cutworm moths are sometimes treated with pesticides, bioaccumulation in the moths and subsequent transport of these chemicals to the alpine (where bear feeding occurs) was of potential concern. Robison et al. (2006) sampled moths in the alpine to analyze for pesticide residues and illustrated that moths only contained pesticides in trace amounts. Furthermore, calculations based on the bears’ estimated consumption of the moths indicated that bears did not consume enough moths to reach physiological toxicity.

High elevation ecology

Army cutworm moths were initially thought to be bivoltine in an effort to explain their sudden disappearance during the summer months and later reappearance in the fall; however, this explanation failed to establish why there were never fully formed ova in the spring brood and the reduced population size in the fall (Gillette, 1903; Johnson, 1905). Cooley (1916a) demonstrated in Montana that army cutworm moths reared at ambient summer temperatures were mostly unable to survive through the end of summer and thus it was theorized that the moths aestivated during the summer months (Cook, 1927; Pepper, 1932).

Observation of a unidirectional flight in southwest Montana during the spring indicated that the moths may migrate in response to deteriorating conditions (increased temperatures) in the Great Plains, instead of aestivating during the summer (Pepper, 1932). Discovery of the moths in large numbers at high elevation in talus fields corroborated this hypothesis (Chapman et al., 1955), and an illustration of the moths' ability to sustain flight after feeding on nectar resources indicated migration of such distances was possible (Koerwitz & Pruess, 1964). Pruess and Pruess (1971) used another method to document unidirectional migration with simultaneous telescope observations in North Platte, Nebraska and Laramie, Wyoming. With an observer stationed at each location, the authors tracked moths outlined against the moon and estimated the flight direction, height, and vertical distribution of the moths. Blacklight traps were used to confirm the identity of the migrants. Pruess and Pruess (1971) noted that moths were flying westward, often independent of the prevailing ground-level wind direction.

En route to the mountains, army cutworm moths are thought to migrate in a “leap-frog” pattern, using conducive weather fronts to assist their flight and stopping periodically to feed on nectar sources (O'Brien & Lindzey, 1994). During this period of spring migration, moths have been spotted flying low to the ground, feeding on flowers (Kevan & Kendall, 1997). Pruess asserted that the return flight coincides with fall Pacific cold fronts, which likely result in a faster return trip to the plains (personal communication between Pruess and O’Brien, 1994). Energy stores remaining after the re-migration suggest that flight is assisted; White et al. (1996) found that after the return flight, moths captured in north-central Montana had lipid stores that were only 30% depleted.

This method of weather-assisted migration occurs in several different migratory noctuids. The black cutworm (*Agrotis ipsilon*, Hufnagel) has been shown to use weather-assisted migration (migrating in a north-south orientation instead of east-west), after it was demonstrated that synoptic weather patterns could be used to predict the relative displacement and arrival of these migrants (Showers et al., 1989). These flights are thought to occur below 1500 m (between 300-900 m), which occurs in the range of the atmospheric low-level jet (Showers et al., 1989a). The low-level jet occurs in the boundary layer wind profile that is common to the Great Plains; it is strongest during the night and primarily moves in a northerly and southerly orientation (Arritt et al., 1997; Shapiro & Fedorovich, 2008; Shapiro et al., 2016; Song et al., 2005; Walters et al., 2008). It is likely that the army cutworm moth migrates at a similar altitude, using synoptic weather patterns that instead occur in an east-west orientation.

The army cutworm moth exhibits oogenesis flight syndrome (French et al., 1994; Kevan & Kendall, 1997; Pruess & Pruess, 1967). Before and during migration to the Rocky Mountains, females lack developed ova (Kevan & Kendall, 1997). Similarly, males are not attracted to pheromone traps at this time, indicating their sexual immaturity. When in the mountains, moths forage on alpine flowers primarily during the night, although feeding has also been observed to occur during the day in the wetter summer months (French et al., 1994; Kevan & Kendall, 1997; White et al., 1998b; personal observation). This food source is then metabolized into lipids that are stored in the abdomen, aiding in remigration and future oogenesis (French et al., 1994; Kevan & Kendall, 1997; White et al., 1998b). Lipid content, as a percentage of body weight, can reach as much as 85% toward the end of the summer (before remigration) whereas newly emerged adult moths generally have 20-34% abdominal lipid content (Kevan & Kendall, 1997; Pruess & Pruess, 1967). These large increases in lipid content suggest that moths are likely not flying far to feed (personal observation).

Toward the end of the summer, few moths mate before re-migration in the Glacier National Park (GNP) area and in the mountains of Colorado (Kevan & Kendall, 1997; White et al., 1998b). Few females are found with maturing eggs in late summer in these areas, and reproductive maturity begins in the late summer. Conversely, in the GYE moths begin to mate around mid-July to mid-September in large numbers (French et al., 1994; Robison, 2009).

Methods for tracking migration

Previous methods

Prior to our work, the relationship between natal origin of the army cutworm and its respective summer destination (in the Rocky Mountains) was unknown. Only one method has been used to determine the origin of the moth. Using an analysis of three DNA microsatellites in moths collected from both the peaks and low elevations, Robison (2009) found that the moths are panmictic and capable of dispersing throughout the entirety of the Rocky Mountains. This finding is unsurprising because, for insects, it is difficult to establish migratory patterns using genetic studies given that interbreeding prevents populations from attaining distinctive genetic differences (Endler, 1973).

O'Brien and Lindzey (1994) suggested the use of pollen to track where the moths originated, as was done with *Helicoverpa zea* (Boddie), commonly known as bollworms, by Hendrix III et al. (1987). An understanding of the regional chronology of green-up facilitated the analysis of the pollen on which the moths were feeding. This technique could provide an estimate of the general region where the larvae were feeding, but it is limited to this generalization only (unless the biome in which the larvae were feeding was restricted to a specific area).

Radar

Radar is a means to measure and characterize features of insect migration that indirect observations of migration (e.g. blacklights paired with ground observations) cannot provide, such as the height at which the insects are flying, the mass of the insects, and the displacement of the insects (Chapman et al., 2003). Preliminary studies during the 1970s and 1980s were primarily conducted with the use of X-band scanning radar (Chapman et al., 2011), in which the focus was often agricultural pests (Reynolds & Riley, 1997). These initial studies illustrated the spatial and temporal distribution of migrants, in addition to insect displacement, speed, and orientation behavior (Reynolds & Riley, 1997). Long-distance migration of noctuid moth species were often considered, and long-term studies were undertaken to provide a better understanding of *Helicoverpa zea* (Westbrook, 2008). The use of meteorological technology concurrently with radar also made for advances in understanding insects' use of synoptic weather patterns—focusing on noctuid-sized insects, Beerwinkle et al. (1994) illustrated that the majority of these insects flew in the nocturnal low-level wind jet.

The U.S. national network of WSR-88D Doppler radars (primarily installed for tracking weather) has also been used to assess noctuid migration, although they lack the resolution to distinguish individual noctuid moths (Westbrook & Wolf, 1998). This equipment operates similarly to X-band radars and is capable of detecting ground speed as well as displacement direction of migrating noctuids (in conjunction with measures of precipitation and weather) (Crum & Alberty, 1993; Westbrook, 2008). If the correct target information was acquired (used to distinguish the target of interest from other migrant bioflows and noise), documented data from these radars could be used to discern migratory patterns of an insect for the past decade (Robb Diehl, personal communication, 28 March 2020).

In the 1990s, technological advancements such as the inception of Vertical Looking Radar (VLR) and harmonic radar facilitated more detailed study of insect migrants (Chapman et al., 2011). Harmonic radar is likely too large for most noctuids, and thus the focus in this review remains on other radar methods, such as VLR and X-band radar. With VLR came the ability to distinguish individual insects according to wingbeat frequency, maximum reflectance to minimum reflectance ratio, and shape. Using this information to discern which of the signals is likely the target, the target's horizontal speed, displacement direction, body alignment, and estimate of body mass and shape could be discerned (Chapman et al., 2003).

In the context of migratory noctuids, major developments included the discovery that these moths can orient their flight and generally fly downwind, although the mechanism of this orientation remains unknown (Wood et al., 2006). Studies of *Autographa gamma* (Linnaeus), a noctuid that migrates between Africa and northern Europe, indicate the potential for an internal compass that aids in the selection of conducive winds (Chapman et al., 2008a). Such findings may suggest similar mechanisms in the migration of *E. auxiliaris*, and characterization of the height of flight may provide more insight about what synoptic weather patterns this moth may be using.

Stable isotope analysis

Stable isotopic analysis is a method of analysis that continues to experience increased use in entomological studies (Hobson et al., 2018). Although advances have been made in understanding the ecology of long-distance migrants using exogenous markers such as radio or satellite transmitters and metal or color tags (Webster et al., 2002), these markers are typically too large for insects or re-encounter rates are too infrequent (Hobson & Norris, 2008). Mark-recapture offers an alternative to geolocators and transmitters, but this method is often time- and resource-intensive, yielding few results (Hobson et al., 2003). Instead, the analysis of naturally occurring endogenous markers—stable isotopes—is a means to determine the origins of migrants through an understanding of how these markers are processed and assimilated in the organism and referenced against the spatial patterns predicted (and observed) to occur in an “isoscape” (Wunder, 2010).

For holometabolous species such as moths, chitinous structures that are not metabolically active (e.g. wings) retain the isotopic signature of their larval stage, which in turn reflects the isotopic signature of larval food sources (Wassenaar & Hobson, 1998). Commonly used isotopic signatures in entomological studies include hydrogen, carbon, nitrogen, oxygen, and sulfur (Wassenaar, 2009). Each isotope offers insight on different aspects of the organism’s biome—an enriched nitrogen value indicates that the organism originated from an agriculturally intensive region, whereas stable carbon values can be used to differentiate between whether a larvae was feeding on plants with a C3 or C4 profile (Hobson et al., 2018; Marshall et al., 2007). Examining the hydrological profile (stable hydrogen and stable oxygen) of an insect is a means to determine origin when comparing those values to a hydrological isoscape (Hobson et al., 2018). Isoscapes for hydrological profiles continue to improve and have been established for both precipitation and tapwater (Bowen et al., 2007; Brattström et al., 2010; Terzer et al., 2013).

One of the preliminary insect migration studies using isotopic analysis followed the migratory patterns of the monarch butterfly (*Danaus plexippus*, Linnaeus): by rearing monarch butterflies on local milkweed (exclusively on local precipitation) throughout the butterflies' natal region in North America, a wing isotopic signature for stable hydrogen (δ^2H) and carbon (δ^{13}C) was created for this region (Wassenaar & Hobson, 1998). This wing isoscape was then used to identify the origin of monarchs captured in their wintering location in Mexico (Hobson et al., 1999) and in a number of other studies to establish critical components of monarch butterfly ecology.

This method has been used in determining the ecology of several other migrants; to reduce the logistical constraints of the study, closely related insects were used to model the predicted isoscape for the insect of interest. The red admiral (*Vanessa atalanta* L.) undertakes a complex and highly variable migration. To establish where this species reproduces (in addition to a number of other critical ecological pieces), expected values of stable hydrogen (δ^2H) for this butterfly were established by combining data from butterfly species endemic to Capri and butterflies developed in Sweden (Brattström et al., 2010).

The δ^2H isoscape generated for the study of the red admiral was also used to determine the origin of the painted lady (*Vanessa cardui* L.) by re-calibrating the isoscape using known-origin butterflies from throughout the Palearctic (Stefanescu et al., 2016). Similarly, a North American dragonfly wing isoscape (for (δ^2H and δ^{18}O) was derived from the collection of three known-origin species of dragonfly throughout North America. To illustrate proof of concept, the isoscape was used to map the predicted natal origin of common green darners (*Anax junius* Drury) (Hobson et al., 2012).

Although ideal, rearing the insect of interest or collecting the insect throughout its entire natal region to generate an isoscape is often unrealistic for many researchers. Probabilistic assignment (or Bayesian assignment) is an alternative to these methods, and this method was used to establish the origin of true armyworms (*Mythimna unipuncta*, Haworth). The stable hydrogen (δ^2H) values of lab-reared armyworms (raised on several different values of δ^2H diets) were calibrated with amount-weighted precipitation to generate a δ^2H_{wing} isoscape, which was "capped" using the known geographic range of the armyworm (Hobson et al., 2018). These studies are thus limited by the accuracy of the predicted isoscape as well as the understanding of how an isotopic value may change when it is assimilated from food sources (and similarly, from the environment by producers) (Brattström et al., 2010).

Alpine moth aggregation sites

Characteristics of moth aggregation sites

After reaching their alpine summer location, moths hide in the talus during the day (French et al., 1994; Kevan & Kendall, 1997; O'Brien & Lindzey, 1994; White et al., 1998a, 1998b). When examining the characteristics of moth aggregation sites throughout the Rockies, the following features have been observed as common: water, geomorphological features, slope, aspect, and elevation. Although other variables tend to shift according to regionally specific factors (such as climate), common to all moth aggregation sites is moisture. Throughout the summer, the location of moth aggregations throughout the talus changes to reflect water availability (French et al., 1994; O'Brien & Lindzey, 1994; Robison, 2009; White, 1996). In addition to preventing desiccation in an otherwise arid climate, the presence of water in talus likely creates the correct temperature gradient the moths require (White et al., 1998b).

Similarly, the geology of moth sites throughout most regions is commonly characterized by bare talus fields located beneath parent rock, such as glacier cirques, cols, and aretes (French et al., 1994; Mattson et al., 1991; O'Brien & Lindzey, 1998). In the GYE, talus also must be of a certain depth and size for moth accumulations to occur. Robison (2009) noted that although surficial geology might indicate the presence of moths, these potential sites would not contain moths if the talus was too shallow; she estimated this was due to the lack of a thermal gradient that facilitated thermoregulation. This temperature gradient is described by White et al. (1998a). Similarly, O'Brien and Lindzey (1994) found that higher moth abundance generally occurred in areas of deeper talus (as much as 40 cm), and noted that few moths were found in talus of depths 0-15 cm. Rock size of the talus fields in which the moths inhabit ranges from 6-12 cm in the GYE to 2-100 cm in GNP (French et al., 1994; White, 1996).

Throughout the Rockies, elevation of alpine moth sites primarily ranges from 2700-3500 m (French et al., 1994; Mattson et al., 1991; White et al., 1998a), while the primary aspect on which moths can be found shifts when moving from the northern Rocky Mountains to the southern Rocky Mountains. Although moths are not limited to one aspect, moths are most commonly found on south and southwestern (warmer) aspects in the northern Rockies (Mattson et al., 1991; White et al., 1998a). This is particularly true of the GYE: O'Brien and Lindzey (1994) noted that moths occurred on all aspects except for northerly sites and were most commonly found on southern facing sites (136-221°), although French et al. (1994) found moth aggregation sites on northeast, northwest, southeast, and southwest aspects. These studies, however, did not assess the significance of the influence of aspect on where moths tended to aggregate. Conversely, in the southern Rockies, moths were found on western to northwestern aspects (Coop et al., 2005).

Another critical component that likely influences the location of moth aggregation sites is the presence of alpine flowers nearby. Although the relationship between the distance of flowering vegetation and where moths accumulate has not been explored (Robison, 2009), flowering vegetation is present in all alpine moth sites that have been recorded except for the St. Jemez mountains of New Mexico, where moths may have to fly farther to forage for nectar (Coop et al., 2005). In the Colorado mountains, moths were captured while feeding on *Salix* spp., *Phlox condensata*, *Haplopappus lyallii*, *Smelowskia calycina*, *Thlaspe alpestre*, *Mertensia* spp., *Valeriana capitata*, and *Polygonum bistorta*; pollen contained in the proboscis was used to confirm these species (Kendall, 1981; Kevan & Kendall, 1997). Although there is no documentation of what species the moths feed on in GNP, this alpine plant community also contains an abundance of forbs, such as *Erythronium grandiflorum*, *Polygonum bistortoides*, and *Dryas hookeriana* (White, 1996).

Thilenius and Smith (1985) extensively documented the flora of the GYE and noted a strong presence of forbs. Mattson et al. (1991) noted that these alpine tundra-covered benches and plateaus often occurred above and below many of the moth sites, and again a number of nectareous plants were observed. Previous efforts of blacklight capture in the valley below Francs Peak indicate that moths were not flying to lower elevations to forage on nectar despite an abundance of flowering vegetation. Furthermore, it was noted that flowers were abundantly dispersed throughout or near talus sites, and it is likely that moths are not flying far to feed (personal observation).

Moth feeding habits were then tentatively established by French et al. (1994), in which moths were recorded to feed on green bluebell (*Mertensia lanceolata*), thick-leaved groundsel (*Senecio crassulus*), mules-ears (*Wyethia amplexicaulis*) and elephant's head (*Pedicularis groenlandica*). Similarly, Robison (unpublished data, 2009) noted that feeding habits indicated that the moths were generalists. Thus, although rising temperatures may threaten some alpine flower species, the generalist feeding habits of the moth likely protect it against changing plant community composition at alpine sites.

Temporal abundance and measuring moth abundance at alpine sites

Moths begin to arrive in the alpine locations during summer at the time when enough snow has melted into interstitial talus and the flowering of alpine species has made nectar resources available (French et al., 1994; Mani, 1962). In the northern Rocky Mountains, arrival in the alpine has been observed to occur primarily in late June and July (French et al., 1994; Kendall, 1981; White, 1996). Within the GYE, moth arrival occurs in late June and early July, and abundance peaks with the availability of alpine nectar resources (typically in late July and early August) (Mattson et al., 1991; O'Brien & Lindzey, 1994). Departure for the Great Plains occurs after nectar resources have dwindled (Kendall, 1981) and, in the GYE, most moths depart from the alpine locations in early September (again, contingent on weather and nectar resources) (O'Brien & Lindzey, 1994). These temporal estimates were primarily established with blacklight trapping (Kendall et al., 1981; Kevan & Kendall, 1997; O'Brien & Lindzey, 1994; White, 1996; White et al., 1998b).

Although the moths' temporal dynamics at alpine sites are understood, representative measures of density at alpine moth sites have been more difficult to obtain, and long-term population dynamics of the moth are entirely lacking. In GNP, measures of density were established through sampling per square meter in moth aggregation sites—averages ranged from 6-15 moths/m^2, but these numbers could reach as high as 178 moths/m^2 in areas of higher moth density. A similar method was attempted in the GYE, but no numbers were reported (French et al. 1994). O'Brien and Lindzey (1994) conducted hand-searches in the talus, but these efforts were limited and yielded few results.

These authors noted that hand-excavated estimates were complicated by variable moth mobility that reflected the conditions of the microsite; if sampled at colder temperatures, moths were easier to capture (and thus the sample was more accurate), but if sampled at warmer temperatures, moths could easily climb under the talus or fly away. To circumvent this issue, Erik Peterson used handheld vacuums when sampling (Erik Peterson, personal communication, 27 February 2020). Furthermore, the depth of the talus is variable, and it is not always possible to dig until ice or soil is reached.

This paucity of moth population data is not without reason: sampling moths in the alpine is complicated by time and effort required to reach these remote sites, potential displacement of foraging bears, and threats to personal safety. Moth sites are scattered heterogeneously throughout the landscape and are often difficult and time-consuming to reach, and this process is only further complicated when paired with transporting blacklight supplies to a site. To increase efficiency of searching for moth sites, Robison (2009) created a Resource Selection Function (RSF) model for moths in the GYE but determined that her model was biased toward the interaction of moths and bears. Thus, to provide a representative estimate of density for a particular region, sampling efforts must be conducted both extensively and intensively throughout the area of interest, and to establish a long-term assessment of moth populations in the alpine using these methods would be resource- and time-intensive.

Objectives

My study had four objectives: (1) identify the probable natal origins of army cutworm moths collected at moth aggregation sites of interest using a $\delta^{2}H_{wing}$ isoscape and characterize the agricultural intensity of the source region and larval feeding habits of collected migrants using $\delta^{15}N$ wing measurements and $\delta^{13}C$, respectively; (2) identify the migratory routes of army cutworm moths collected throughout the Great Plains during their spring and fall migratory period using a $\delta^{2}H_{wing}$ isoscape; (3) verify the assumption that the isotopic signature of moth wings remains unchanged after feeding as an adult; and (4) establish an estimate of army cutworm moth abundance using radar at a moth aggregation site of interest.

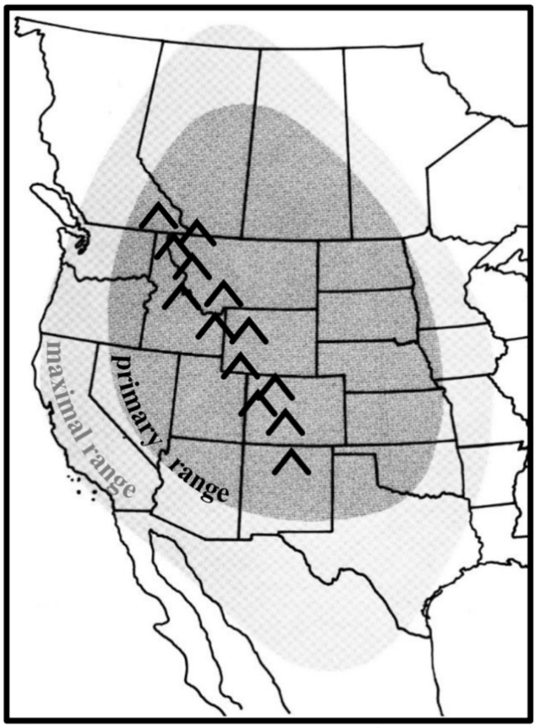


Figure 1: Army cutworm moth range, adapted from Burton et al. (1980) by Nunlist (2020a).

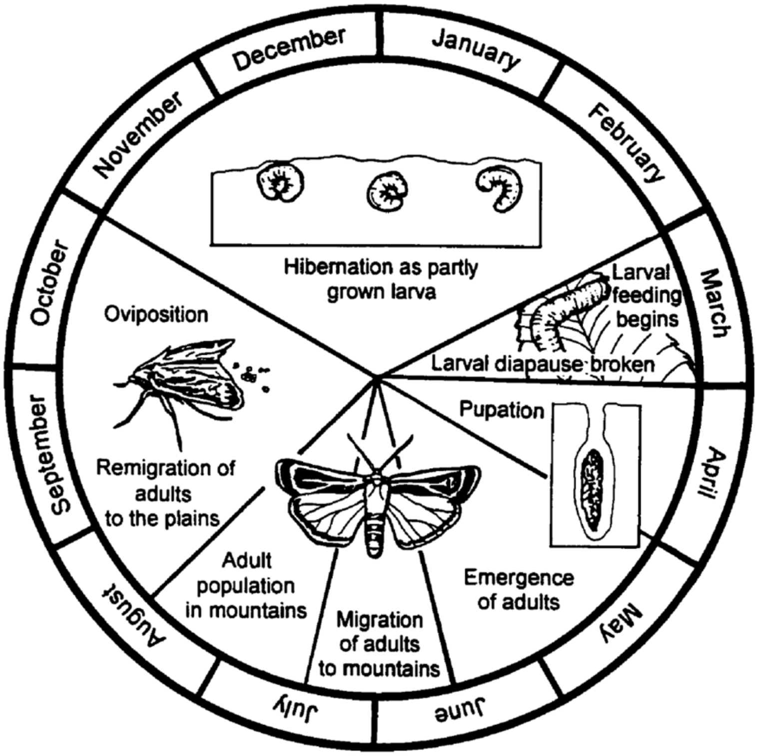


Figure 2: The life cycle of the army cutworm moth, from White (1996) and modified from Kendall (1981).

REFERENCES CITED

Arritt, R. W., Rink, T. D., Segal, M., Todey, D. P., Clark, C. A., MItchell, M. J., & Labas, K. M. (1997). The Great Plains low-level jet during the warm season of 1993. *Monthly Weather Review, 125*, 2176-2192.

Beerwinkle, K. R., Lopez, J. D., JR., Witz, J. A., Schleider, P. G., Eyster, R. S., & Lingren, P. D. (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, B. P. (1970). Effects of precipitation on crop insects. *The Canadian Entomologist, 102*(11), 1360-1373.

Blodgett, S. (1997). *Pheromone traps help forecast cutworm moth activity* (Montana Crop Health Report, Issue.

Blodgett, S., Lanier, W. T., & Johnson, G. D. (2003). *IPM Western Region Cutworm Survey and Risk Warning 2003 Report*. Montana State University. http://scarab.msu.montana.edu/Cutworm/CW2003.htm

Bowen, G. J., Ehleringer, J. R., Chesson, L. A., Stange, E., & Cerling, T. E. (2007). Stable isotope ratios of tap water in the contiguous United States. *Water Resources Research, 43*(3).

Brattström, O., Bensch, S., Wassenaar, L. I., Hobson, K. A., & Åkesson, S. (2010). Understanding the migration ecology of European red admirals Vanessa atalanta using stable hydrogen isotopes. *Ecography, 33*(4), 720-729.

Burton, R. L., Starks, K., & Peters, D. (1980). The Army Cutworm. *Oklahoma Agricultural Experiment Station*(Bulletin No. B749).

Chapman, J. A., Romer, J. I., & Stark, J. (1955). Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology, 36*(1), 156-158.

Chapman, J. W., Drake, V. A., & Reynolds, D. R. (2011). Recent insights from radar studies of insect flight. *Annual Review of Entomology, 56*, 337-356.

Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology, 18*(19), R908-R909.

Chapman, J. W., Reynolds, D. R., & Smith, A. D. (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

Cook, W. C. (1927). Studies in the ecology of Montana cutworms (Phalaenidae). *Ecology, 8*, 158-173.

Cooley, R. A. (1916). Observations on the life history of the army cutworm, Chorizagrotis auxiliaris. *J. Agric. Res, 6*, 871-881.

Coop, J. D., Hibner, C. D., Miller, A. J., & Clark, G. H. (2005). Black bears forage on army cutworm moth aggregations in the Jemez Mountains, New Mexico. *The Southwestern Naturalist, 50*(2), 278-281.

Crum, T. D., & Alberty, R. L. (1993). The WSR-88D and the WSR-88D operational support facility. *Bulletin of the American Meteorological Society, 74*(9), 1669-1688.

Endler, J. A. (1973). Gene flow and population differentiation. *Science, 179*, 243-250.

French, S. P., French, M. G., & Knight, R. R. (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, C. P. (1903). *Some of the more important insects of 1903* (Vol. 94). Bulletin of the Colorado Agriculture Experiment Station

Hardwick, D., & Lefkovitch, L. (1971). Physical and biotic factors affecting Euxoa species abundance in western North America: a regression analysis. *The Canadian Entomologist, 103*(9), 1217-1235.

Hendrix III, W., Mueller, T., Phillips, J., & Davis, O. (1987). Pollen as an indicator of long-distance movement of Heliothis zea (Lepidoptera: Noctuidae). *Environmental entomology, 16*(5), 1148-1151.

Hobson, K., Wassenaar, L. I., Mila, B., Lovette, I., Dingle, C., & Smith, T. B. (2003). Stable isotope as indicators of altitudinal distributions and moevments in an Ecuadorean hummingbird community. *Oecologia, 136*, 302-308.

Hobson, K. A., Doward, K., Kardynal, K. J., & McNeil, J. N. (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.

Hobson, K. A., & Norris, D. R. (2008). *Animal migration: a context for using new techniques and approaches. Tracking animal migration with stable isotopes*. Academic Press.

Hobson, K. A., Soto, D. X., Paulson, D. R., Wassenaar, L. I., & Matthews, J. H. (2012). A dragonfly (δ2H) isoscape for North America: a new tool for determining natal origins of migratory aquatic emergent insects. *Methods in ecology and evolution, 3*(4), 766-772.

Hobson, K. A., Wassenaar, L. I., & Taylor, O. R. (1999, 1999/08/01). Stable isotopes (δD and δ13C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia, 120*(3), 397-404. https://doi.org/10.1007/s004420050872

Jacobson, L. A., & Blakeley, P. E. (1959). Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America, 52*(1), 100-105.

Johnson, S. A. (1905). Cutworms. *Colorado Experiment Station Bulletin, No. 98*.

Kendall, D. M. (1981). *Bionomics of Euxoa auxiliaris Grote (Lepidoptera: Noctuidae) in the Rocky Mountains and comparison with two resident species of alpine moths* University of Colorado (at Colo. Spgs.].

Kendall, D. M., Kevan, P. G., & LaFontaine, J. D. (1981). Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist, 113*(7), 607-614.

Kevan, P. G., & Kendall, D. M. (1997, 1997/11/01). 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://doi.org/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.

Mani, M. S. (1962). *Introduction to High Altitude Entomology*. Methuen & Co.

Marshall, J. D., Brooks, J. R., & Lajtha, K. (2007). *Sources of variation in the stable isotopic composition of plants*. Blackwell.

Mattson, D. J., Gillin, C. M., Benson, S. A., & Knight, R. R. (1991). Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology, 69*(9), 2430-2435.

Morrill, W. (1991). Montana small grain insects: armyworms and cutworms. *Montana Agriculture Experiment Station, Montana State University, Bozeman, Capsule Information Ser*(34).

Nunlist, E. (2020). *Grizzly Bears and Humans at Two Moth Aggregation Sites in Wyoming* Montana State University]. Bozeman, Montana.

O'Brien, S. L., & 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.

O'Brien, S. L., & Lindzey, F. G. (1998). Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*, 427-435.

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.

Pruess, K., & Pruess, N. C. (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.

Pruess, K. P., & Pruess, N. C. (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.

Reynolds, D., & Riley, J. (1997). *Flight behaviour and migration of insect pests. Radar studies in developing countries*. Natural Resources Institute (NRI).

Robison, H. L. (2009). *Relationships between Army Cutworm Moths and Grizzly Bear Conservation* University of Nevada, Reno].

Robison, H. L., Schwartz, C. C., Petty, J. D., & Brussard, P. F. (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.

Seamans, H. (1928). Forecasting Outbreaks of the Army Cutworm (Chonzagrotis auxiliaris, Grote). *Forecasting Outbreaks of the Army Cutworm (Chonzagrotis auxiliaris, Grote).*

Shapiro, A., & Fedorovich, E. (2008). Coriolis effects in homogeneous and inhomogeneous katabatic flows. *Quarterly Journal of the Royal Meteorological Society, 134*.

Shapiro, A., Fedorovich, E., & Rahimi, S. (2016). A Unified Theory for the Great Plains Nocturnal Low-Level Jet. *Journal of Atmospheric Sciences, 73*, 3037-3057.

Showers, W. B., Smelser, R. B., Keaster, A. J., Whitford, F., Robinson, J. F., Lopez, J. D., & Taylor, S. E. (1989a). Recapture of marked black cutworm (Lepidoptera: Noctuidae) males after long-range transport. *Environmental entomology, 18*(3), 447-458.

Showers, W. B., Whitford, F., Smelser, R. B., Keaster, A. J., Robinson, J. F., Lopez, J. D., & Taylor, E. S. (1989). Direct Evidence for Meteorologially Driven Long-Range Dispersal of an Economically Important Moth. *Ecology, 70*, 987-992.

Snow, S. J. (1925). Observations on the cutworm, *Euxoa auxiliaris* Grote, and its principal parasites. *Journal of Economic Entomology, 18*(4), 602-609.

Song, J., Liao, K., Coulter, R. L., & Lesht, B. M. (2005). Climatology of the low-level jet at the Southern Great Plains Atmospheric Boundary Layer Experiments site. *Journal of Applied Meteorology 44*, 1593-1606.

Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016). Long-distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology letters, 12*(10), 20160561.

Strickland, E. H. (1916). *The Army Cutworm: Euxoa (Chorizagrotis) Auxiliaris Grote* (Vol. Bulletin 13). Canadian Department of Agricultural Entomology.

Terzer, S., Wassenaar, L. I., Araguás-Araguás, L. J., & Aggarwal, P. K. (2013). Global isoscapes for δ18O and δ2H in precipitation: improved prediction using regionalized climatic regression models. *Hydrology and Earth System Sciences, 17*(11), 4713-4728. https://doi.org/10.5194/hess-17-4713-2013

Thilenius, J. F., & Smith, D. R. (1985). Vegetation and soils of an alpine range in the Absaroka Mountains, Wyoming. *US Dept of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station*, 1-23.

University of Nebraska, L. (2020). *Light Trap Data*. https://entomology.unl.edu/fldcrops/lightrap

USDA. (1951-1975). Cooperative Economic Insect Report.

Walkden, H. H. (1942). *Owlet moths (Phalaenidae) taken at light traps in Kansas and Nebraska*. US Department of Agriculture.

Walkden, H. H. (1950). *Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains*.

Walters, C. K., Winkler, J. A., Shadbolt, R. P., Ravensway, J. v., & Bierly, G. D. (2008). A long-term climatology of southerly and northerly low-level jets for the central United States. *Annals of the American Association of Geographers, 98*, 521-552.

Wassenaar, L. (2009). *Manual for the Use of Stable Isotopes in Entomology*. International Atomic Energy Agency.

Wassenaar, L. I., & Hobson, K. A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences, 95*(26), 15436-15439.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution, 17*(2), 76-83.

Westbrook, J., & Wolf, W. (1998). Migratory flights of bollworms, Helicoverpa zea (Boddie), indicated by Doppler weather radar. Preprints-Weather Data Requirements for Integrated Pest Management: 23rd Conference on Agricultural and Forest Meteorology, 2nd Urban Environment Symposium, and 13th Conference on Biometeorology and Aerobiology,

Westbrook, J. K. (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, D. D. (1996). *Two grizzly bear studies: moth feeding ecology and male reproductive biology* [PhD, Montana State University-Bozeman, College of Letters & Science].

White, J., Don, Kendall, K. C., & Picton, H. D. (1998a). Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology, 76*(2), 221-227.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998b). Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology, 76*(5), 835-842.

Wood, C. R., Chapman, J. W., Reynolds, D. R., Barlow, J. F., Smith, A. D., & Woiwod, I. P. (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.

Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In *Isoscapes* (pp. 251-270). Springer.

CHAPTER TWO

ESTIMATING THE NATAL ORIGINS AND FEEDING HABITS OF THE ARMY CUTWORM MOTH (*EUXOA AUXILIARIS*) WITH STABLE ISOTOPES

Contribution of Authors and Co-Authors

Author: Clare M. Dittemore

Contributions: Wrote manuscript for journal submission, conceived and designed experiments, recorded and processed experimental data, analyzed and interpreted results, and organized information for interpretation.

Co-Author: Daniel Tyers

Contributions: Edited succeeding drafts of the manuscript.

Co-Author: David K. Weaver

Contributions: Provided intellectual input for analysis and edited succeeding drafts of the manuscript.

Co-Author: Robert K.D. Peterson

Contributions: Provided intellectual input for analysis and edited succeeding drafts of the manuscript.

Co-Author: Erika A. Nunlist

Contributions: Conceived experiment.

Manuscript Information

Clare M. Dittemore, Robert K. D. Peterson

[Type name of journal here]

Status of Manuscript: [Put an x in one of the options below, delete this]
__X_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-reviewed journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

CHAPTER TWO

ESTIMATING THE NATAL ORIGINS AND FEEDING HABITS OF THE ARMY CUTWORM MOTH (*EUXOA AUXILIARIS*) WITH STABLE ISOTOPES

Abstract

The army cutworm, *Euxoa auxiliaris*, is a migratory noctuid with the unusual dual status of agricultural pest and an important food source for grizzly bears, *Ursus arctos horribilis*, within the Greater Yellowstone Ecosystem. Beyond the confirmation of the moths' seasonal, altitudinal migration in the mid-1900s, little else has been documented about their migratory patterns. Therefore, management of this grizzly bear food source has been difficult. To address this missing ecological component, we attempted to characterize: (1) migratory pathways during their spring and fall migratory periods throughout their natal range, the Great Plains, and (2) natal origin at two of their summering ranges, the Absaroka and Lewis Range, using stable hydrogen (δ^2H) analyses of wings from samples collected within the areas of interest. Stable carbon (δ^{13}C) and stable nitrogen (δ^{15}N) analyses of wings were used to evaluate larval feeding habits of the migrants and agricultural intensity of natal origin sites, respectively. Results suggest that, in addition to previously documented east-west movement, army cutworm moths are also migrating north-south during their spring migratory period. Moths did not exhibit natal-origin site fidelity when migrating back to the Great Plains. Natal origin of moths collected at their summering ranges indicated that most migrants of the Absaroka Range had the highest probability of origin within Alberta, British Columbia, and Saskatchewan, and the most southern region of the Northwest Territories. Within the United States, Montana, Wyoming, and Idaho,

whereas migrants collected in the Lewis Range had probable origins of almost exclusively Canada, extending into the southern border of the Northwest Territories. Results suggest that migrants of the Absaroka Range fed as larvae exclusively on C3 plants and few individuals fed in heavily fertilized agroecosystems. Because army cutworm moths had varied origins within the Absaroka Range, this important grizzly bear summer food source is likely protected against a potential population declines.

Introduction

As a migratory noctuid, the army cutworm moth, *Euxoa auxiliaris* (Lepidoptera: Noctuidae) plays two roles during its one-year life cycle. During their larval stage, army cutworms are serious, yet sporadic generalist agricultural pests with a range that spans the Great Plains (Burton et al., 1980). Larvae hatch in the fall to feed on a wide variety of crops and weed species and develop to their second or third instar before overwintering in the soil near their plant hosts. After their overwintering period, larvae become active in the spring to continue feeding until reaching their sixth or seventh instar (Burton et al., 1980; Seamans, 1928b; Strickland, 1916; Walkden, 1950). Pupation then occurs and adults emerge in the late spring and early summer and migrate at night west to high elevations in the Rocky Mountains, escaping the hot summer temperatures and dwindling resource availability of their natal range (Hardwick & Lefkovitch, 1971; Jacobson & Blakeley, 1959; Pruess & Pruess, 1967). This migration coincides with the flowering of plants along the east-west gradient, and moths are thought to use a “leap-frog” pattern to reach the mountain peaks, periodically stopping to feed on nectar in flowers (Kendall et al., 1981; Kevan & Kendall, 1997; O'Brien & Lindzey, 1994).

Upon reaching the Rocky Mountains, army cutworm moths constitute a significant portion of grizzly bear (*Ursus arctos horribilis*) diets each summer for grizzly bears with home ranges that both encompass moth aggregation sites within the Greater Yellowstone Ecosystem (GYE) and choose to feed at these sites (French et al., 1994; Mattson et al., 1991). Rather than estivate as other migratory noctuids that also exhibit an altitudinal migration do (Common, 1954; Oku et al., 1983; Oku et al., 1982), army cutworm moths roost in the interstitial spaces of the talus during the day and feed on alpine flower nectar during the night (Kendall et al., 1981; Kevan & Kendall, 1997). Moths metabolize ingested nectar into lipid reserves that aid future oogenesis and their return to the Great Plains at the conclusion of the summer (Kevan & Kendall, 1997; O'Brien & Lindzey, 1994; White et al., 1998b).

Grizzly bears forage for these dense aggregations of moths by digging through the talus, a phenomenon that was first documented in 1955 (Chapman et al., 1955). At 0.5 kcal per moth (7.0 kcal/g dry weight), the army cutworm moth is one of the most calorically dense foods in the GYE (French et al., 1994; Mattson et al., 1991; White et al., 1998a), and its availability coincides with a period that is critical for bears to gain fat (Nelson et al., 1983). Provided that moth density is high enough, grizzly bears can consume as many as 40,000 moths per day (White, 1999)—equating to almost half of a bear’s annual energy budget after feeding on moths for 30 days (White, 1996).

Moth aggregation sites have seen an increase in use by foraging grizzly bears since 1986 (IGBST, 2020; Mattson et al., 1991), and given the recent decline in grizzlies’ other critical food sources, such as cutthroat trout, whitebark pine seeds, and ungulates (for some areas) (Fortin et al., 2013; Koel et al., 2005; Manen et al., 2016; Schwartz et al., 2014), the army cutworm moth has likely become increasingly important. However, several components of the ecology of the army cutworm moth remain poorly understood despite their importance in grizzly bear diets.

Although there are several theories on how natal origin of army cutworm moths affects which peaks the moths select for over-summering, to date, only a single study has attempted to provide a better understanding of its migratory patterns. Using three microsatellites (groups of repetitive, non-coding genes) in moths collected both at peaks of conservational interest and at lower elevations, Robison (2009) demonstrated that the moths were panmictic. This finding was consistent with the limitations of genetic studies done on migratory insects because interbreeding often prevents populations from attaining distinctive genetic differences (Endler, 1973).

Therefore, concerns remain regarding whether moth populations at aggregation sites are supplied by a variety of locations or a small source location (e.g., the Bighorn Basin for the moth aggregation sites located in the Absaroka Mountain Range, as White et al., (1996) posited). If the latter is true, a moth aggregation site would be depleted of moths if the site’s respective source population were drastically reduced. In a more extreme instance, although unlikely, extirpation of a local population would equate to a lack of moths at the natal origin site’s corresponding moth aggregation site, forcing bears to forage elsewhere for food.

Of the techniques used for establishing natal origin of migratory insects, the analysis of naturally occurring endogenous markers—stable isotopes—arguably provides the most feasible approach (Wunder, 2010). This technique has seen increased use in entomological studies, although its application has lagged behind other taxa (Quinby et al., 2020). Commonly used isotopes include carbon, hydrogen, nitrogen, oxygen, and sulfur, wherein each marker provides different insight about the organism’s biome (Quinby et al., 2020; Wassenaar, 2009).

Stable hydrogen, or δ^2H, has been used in studies to track insect movement (Brattström et al., 2010; Flockhart et al., 2017; Flockhart et al., 2013; Hobson et al., 2018; Hobson et al., 2022; Hobson et al., 2012; Wassenaar & Hobson, 1998; Yang et al., 2016). The discrimination factor for stable hydrogen is very low, i.e., stable hydrogen in environmental water is incorporated into plant tissues and subsequent plant consumers without significant changes. Thus, because metabolically inert, chitinous tissue (e.g., wings) are representative of larval feeding habits, wings collected from adults can be analyzed and referenced against a map of predicted δ^2H values to determine natal origin of the sample (Hobson et al., 2018; Wassenaar & Hobson, 1998). Stable hydrogen varies systematically and predictably throughout the globe due to patterns in precipitation and the mixing of surface waters, and thus it is a powerful tool when assessing the question of origin (Hobson & Wassenaar, 2019). This is especially true when applied to systems within North America because these patterns are very pronounced on a north-south gradient (Bowen et al., 2005; West et al., 2006; West et al., 2009).

Natal origin studies also frequently employ the use of at least one other isotope to better understand other components of the organism's biome. Stable carbon values, or δ^{13}C have been used to both determine feeding preferences when C3 and C4 plants were present and, for migrants, distinguish whether insects were primarily feeding on C3 or C4 plants (Hobson et al., 2018; Hobson et al., 2022; Hyodo, 2015; Layman et al., 2012; McNabb et al., 2001; Ponsard et al., 2004; Prasifka & Heinz, 2004; Quinby et al., 2020). Stable nitrogen, or δ^{15}N, also provide insight about the organism's feeding habits. Although δ^{15}N values can be complex to interpret due to a variety of factors (Hobson & Wassenaar, 2019; Pardo & Nadelhoffer, 2010), these values have been used to illustrate how agriculturally intensive the organism's natal area is

(Hobson et al., 2018). Given the generalist feeding habits of the army cutworm moth, characterizing major contributing sites (agricultural vs. wildland) would better inform our understanding of the larval ecology of moths that constitute "source populations" in the Great Plains.

The Shoshone Forest Management Plan (USFS, 2015) directs the preparation of a "moth site" management plan with the intent of protecting the ecological integrity of these sites, grizzly bear conservation, and addressing human safety in areas with high bear density. In response, executive managers in the GYE highlighted the need for additional information, including a better understanding of army cutworm moth ecology (TES-GOAL-04; USFS, 2015). Thus, this project was created to address this specific information need and the following research objectives were jointly developed by the USFS (SNF & GYE Grizzly Bear Habitat Coordinator) and Montana State University:

(1) characterize the natal origin of army cutworm moths collected on three different peaks of conservational interest within the Absaroka Range,
(2) determine whether army cutworm moths fed predominantly on C3 or C4 plants, or both in their natal origin sites,
(3) evaluate the agricultural intensity of these natal origin sites, and
(4) characterize the migratory pathways of army cutworm moths as they migrate from and return to the Great Plains.

Consequently, our aim was to establish natal origin and migratory pathways using a precipitation isoscape calibrated with the relationship between true armyworm *Mythimna unipuncta* (Haworth) wing δ^2H values (δ^2H_w), and environmental waters established by Hobson et al. (2018). This isoscape was also used to assess the natal origin of army cutworm moths collected in Glacier National Park. We assessed the agricultural intensity of natal origin sites and determined whether larvae fed in C3 or C4 biomes using δ^{15}N measurements and δ^{13}C values, respectively.

Materials and Methods

Study area

Our study encompassed both the army cutworm moths' natal source region, the Great Plains, and a subset of their summering region within the Absaroka Range and the Lewis Range. The Great Plains extend from the Gulf of Mexico to Canada, bordered by the Rio Grande in the south and the Mackenzie River at the Arctic Ocean in the north. This region lies between the Rocky Mountains to the west and the Interior Lowland of the Canadian Shield to the east, and, within the United States, includes the states Montana, North Dakota, South Dakota, Wyoming, Nebraska, Kansas, Colorado, Oklahoma, Texas, and New Mexico (Basara et al., 2013; Robinson & Dietz, 2020). Broadly, precipitation varies extensively over this expanse (more than 30 cm in the east and potentially fewer than 12 cm in the west), and temperature increases when moving north to south (Basara et al., 2013; Robinson & Dietz, 2020). Climate has been described in more detail previously (Kunkel et al., 2013; Rosenberg, 1987).

About 43.7% of the Great Plains is composed of natural grasslands and shrublands and 40.6% is devoted to cropland (Augustine et al., 2021). Natural vegetation in intact grasslands has been described previously (Augustine et al., 2021), and cropland is composed of a mix of C3 and C4 plants. Notably, the northern half of the Great Plains is primarily dominated by C3 crops (excluding the Corn Belt), including wheat, oat, soybean, and sugar beet. Major corn-producing states include South Dakota, Nebraska, Iowa, Kansas, and Missouri, and major sorghum producers include Kansas and Texas (USDA, 2022).

Of the army cutworm moth's summering region, our study included peaks within the Absaroka Range of northwestern Wyoming and the Lewis Range of northwestern Montana. Within the Absaroka Range, elevation ranges 1830-4006 m, wherein moth site elevations range 2700-3500 m (French et al., 1994; Mattson et al., 1991; White et al., 1998a). The geology of moth sites is dominated by talus fields that lack vegetation and lie beneath cliffs (French et al., 1994; Mattson et al., 1991; O'Brien & Lindzey, 1994). Moth populations are supported by neighboring patches of vegetation and meadows (French et al., 1994). Vegetation, climate, and geology have been described previously for this range (Baker, 1944; Dirks & Martner, 1982; Marston & Anderson, 1991; Sundell, 1993; Thilenius & Smith, 1985; Waddington & Wright, 1974). Within the Lewis Range, elevation ranges 948-3190 m, and its geology, vegetation, and climate have also been described previously (Choate, 1963; Damm, 2001; Finklin, 1986; Willis, 1902).

Sample collection: Great Plains

From 2018-2021, army cutworm moths were collected during their spring migratory period (May to early July) with the help of a collection network that spanned the Great Plains. Our collection network included entomologists, insect enthusiasts, and Forest Service employees located in Montana, North Dakota, South Dakota, Wyoming, Nebraska, Kansas, Colorado, Oklahoma, Texas, and New Mexico. Collection sites were grouped into five ecoregions, including the west-central semiarid prairies, western cordillera, cold deserts, south-central semiarid prairies, and warm deserts (Figure 3). Collectors used either blacklight traps or collected army cutworm moths by hand and euthanized them by either: (1) placing in the freezer or (2) euthanizing with insecticidal strips (e.g., Hot Shot No-Pest Strip Insect Killer Strips®).

From 2020-2021, a subset of our Great Plains collectors deployed pheromone traps baited with Scentry Army Cutworm Lures 12/CS (Great Lakes IPM™) during the fall (late August to early October). Moths collected with pheromone traps were euthanized with insecticidal strips. Samples collected from 2018-2020 were shipped and stored at ambient temperatures, and samples collected in 2021 were shipped at ambient temperatures and stored in the freezer at -20˚C until processing. All samples were stored in 6.35 x 8.89 cm (2.25" x 3.5") paper coin cards; samples stored in the freezer were placed in Ziplock bags. We assessed all samples for signs of degradation (e.g., formation of new material) before processing for laboratory analysis and discarded samples that were degraded. Thirty samples (or the total number of samples if < 30) were randomly selected from each county to prepare for stable isotopic analysis. Data from collections in each ecoregion are summarized in Tables 1 and 2.

Sample collection: Moth aggregation sites (mountain peaks)

From 2017-2021, we hand-collected army cutworm moths from the talus at three moth aggregation sites in the Absaroka Range (Figure 4). Moths were euthanized on site by gently squeezing their thorax. All samples from 2017-2020 were stored in 6.35 x 8.89 cm (2.5" x 3.5") paper coin cards at ambient temperature until processing. Samples from 2021 were stored in the freezer at -20˚C until processing. Samples from Glacier National Park were sent to us by a research team that collected at various moth aggregation sites within the park in 2019 (Figure 5); these samples were shipped and stored as described previously. Peaks cannot be identified here due to disturbance concerns (Nunlist, 2020b). Consequently, sites within the Absaroka Range will be referred to as Peaks A-C, and sites within the Lewis Range will be referred to as Peaks D-J. When possible (as dictated by time constraints), all samples were prepared and analyzed for stable hydrogen. When we were unable to prepare all samples for stable hydrogen analysis, we randomly selected samples from each moth aggregation site. We randomly selected 50 samples from each peak and year to prepare for stable carbon and stable nitrogen analysis (or the total *n* for each peak and year if < 50). Data from army cutworm moths collected at moth aggregation sites are summarized in Tables 3-6.

To validate the assumption that stable hydrogen values do not change with wing-tissue turnover in adulthood, we reared another noctuid—fall armyworm, *Spodoptera frugiperda* (Smith)—on sugar-water treatments with differing δ^2H values (844.65 ± 0.43‰ or -138.86 ± 0.09‰) and evaluated their δ^2H_w measurements for potential changes. Although wing tissue is more metabolically inert than other insect tissues, veins that run through the wings may supply the tissue with material created from what was ingested during adulthood, and thus stable hydrogen wing values may also be representative of adult feeding. We raised two groups (n=60 per group) of fall armyworm at 25 ± 3˚C, 65 ± 10% RH, under LD 14:10 on sugar water with differing δ^2H values. Pupae were purchased from Benzon Research, where all pupae were reared in the same cohort and on the same diet using one source of water (municipal city tap-water). We received pupae several days before they emerged as adults. Pupae were randomly assigned to a group and placed into a 610 x 610 x 610 cm (24” x 24” x 24”) screen cage for their respective treatment group. All moths fed voluntarily and ad libitum. After two weeks, all moths were euthanized by freezing and stored in the freezer at -20˚C until processing for analysis. We randomly selected 10 moths from each treatment to prepare for analysis.

Identification

All moths were identified to the Noctuidae family using characteristic wing venation (Triplehorn et al., 2005) and wing patterns characteristic of army cutworm moths per specimen slides prepared by Lafontaine (1987). Due to time constraints, we were unable to perform species identification via standard genitalia dissection for each sample. We instead verified species identification using mitochondrial gene cytochrome oxidase I (COI) for five randomly selected moths per county or moth aggregation site per year. We removed the legs of each specimen, placed the legs inside of a 1.5-mL centrifuge tube, and shipped the samples on reusable ice packs to R. Simmons at the University of North Dakota (UND). For each specimen, the UND team extracted DNA and amplified COI per Pogue and Simmons (2008). In previous work, all samples collected at moth aggregation sites were *Euxoa auxiliaris*, as identified to species per standard genitalia dissection (French et al., 1994; O'Brien & Lindzey, 1994).

Sample preparation and laboratory analysis

Water treatment δ^2H values were measured by off-axis integrated cavity output spectroscopy (OA-ICOS) using a Los Gatos Research Liquid Water Isotope Analyzer at the Environmental Analytical Lab, Montana State University (Bozeman, Montana).

All wing samples were placed into 20-ml scintillation vials and washed and soaked with a 2:1 chloroform:methanol solution under a fume hood. Samples were left in the fume hood overnight with caps left slightly ajar to allow the solution to air-dry, and any remaining fluid was pipetted out the following day. For stable-hydrogen samples, the left hindwing (when viewed dorsally) was removed from the thorax. Wing subsamples (0.25 ± 0.03 mg) were weighed and pressed into silver 5x3.5-mm capsules (EA Consumables). For stable-carbon and stable-nitrogen samples, the right hindwing was removed from the thorax. If the specimen was missing a right hindwing, the right forewing was removed from the thorax instead. Wing subsamples (0.55 ± 0.04 mg) were weighed and pressed into tin capsules (EA Consumables). All wing samples were sent to the University of New Mexico Center for Stable Isotopes for laboratory analysis (Albuquerque, New Mexico).

Stable hydrogen samples and reference materials were subjected to bench-top equilibration to local water vapor for three weeks before analysis (Wassenaar & Hobson, 2000). Stable hydrogen values of the non-exchangeable portion of hydrogen were determined using comparative equilibration (Wassenaar & Hobson, 2003) using three internal laboratory keratin reference materials. Values of δ^2H for the internal laboratory keratin reference materials were measured by comparative equilibration experiments and externally verified with other laboratories. Laboratory standards were calibrated with keratin standards distributed by USGS Reston, Virginia, including CBS (-157‰), KHS (-35.3‰), USGS 42 (–72.2‰) and USGS 43 (–44.2‰), as revised by Soto et al. (2017).

Stable hydrogen values were determined using a Thermo-Finnigan high-temperature conversion elemental analyzer (TCEA) coupled to a Thermo-Finnigan Delta V Isotope Ratio Mass Spectrometer. Isotopic results are expressed as δ values, using the per mill notation, and calculated as:

$$\delta^2\text{H} = 1000^* \, [(R_{\text{sample}} - R_{\text{standard}}/R_{\text{standard}})],$$

where R_{sample} and R_{standard} are the ^{2}H/^{1}H of the sample and standard, respectively. Precision for δ^2H was determined by the analysis of the three exchangeable (keratin) reference materials described above. Standard deviation (1 SD or 1σ) calculated on repeat analysis of these reference materials was ≤2‰.

Nitrogen and carbon isotope ratios were measured by Elemental Analyzer Continuous Flow Isotope Ratio Mass Spectrometry using a Costech ECS4010 Elemental Analyzer coupled to a ThermoFisher Scientific Delta V advantage mass spectrometer via a CONFLO IV interface. Three internal laboratory standards were run at the beginning, at intervals between samples, and at the end of analytical sessions. Analytical precision calculated from the standards was ± 0.1‰ (1 SD or 1σ) for both δ^{15}N and δ^{13}C. Analyses were normalized to the laboratory standards. Laboratory standards were calibrated against IAEA N1, IAEA N2 and USGS 43 for δ^{15}N and NBS 21, NBS 22 and USGS 24 for δ^{13}C. The three internal laboratory standards used were: UNM-CSI Protein std#1, casein purchased from Sigma Aldrich with δ^{15}N and δ^{13}C values of 6.43‰ and -26.52‰; UNM-CSI Protein std#2, soy protein purchased from Sigma Aldrich with δ^{15}N and δ^{13}C values of 0.98‰ and -25.78‰; and UNM-CSI protein Std#4, house made tuna protein with δ^{15}N and δ^{13}C values of 13.32‰ and -16.17‰.

Statistical analysis

All statistical analyses were performed in R (Team, 2020).

Spring and fall samples. Due to the arbitrary nature of political boundaries as prescribed by counties, we aggregated spring and fall samples into ecoregions per Ecoregion II, a level intended for examining subcontinental ecological trends produced by the U.S. Environmental Protection Agency (Omernik & Griffith, 2014). We fit a linear model between δ^2H_w and ecoregion and year, and we assessed the need for the inclusion of an interaction between ecoregion and year with a two-way ANOVA. We determined that the interaction should be kept, and we flattened the two variables into an ecoregion*year variable. Using a one-way ANOVA, we assessed whether there were differences between ecoregions in mean δ^2H_w and established that there were significant differences between ecoregions. We performed a post-hoc analysis with Tukey's Honest Significant Difference (HSD, $\alpha = 0.05$).

<u>Moth aggregation site samples</u>. We extracted the Bighorn Basin's predicted δ^2H_w value with a 1-degree buffer from the wing tissue-calibrated isoscape. This value was used as the reference value in a two-sample t-test, against which we compared the pooled stable hydrogen mean from moths collected within the Absaroka Range. A linear model was fit between δ^2H_w and moth aggregation site and year. We assessed the need for the inclusion of an interaction between moth aggregation site and year, determined the interaction should be kept, and flattened the interaction into one variable. We examined for differences in mean δ^2H_w between moth aggregation sites and across years by performing a one-way ANOVA on the model and performed a post hoc analysis with Tukey's HSD.

A linear model was fit between $\delta^{13}C$ wing ($\delta^{13}C_w$) values and moth aggregation site/year. Using a two-way ANOVA, we: (1) examined for differences in mean $\delta^{13}C_w$ values between moth aggregation sites and across years, and (2) tested for an interaction between year and moth aggregation site on $\delta^{13}C_w$ values. Significant differences in $\delta^{13}C_w$ values were found between years. We performed a post-hoc analysis with Tukey's HSD. We repeated these steps with stable nitrogen and found no significant differences between years or mountain peaks. There was no evidence for an interaction between year and peak, and we dropped the interaction from the model. Stable hydrogen, stable nitrogen, and stable carbon data are summarized in Tables 3-6.

Natal origin assignment. To assign natal origin of moths collected at moth aggregation sites during the spring migratory period and during the fall migratory period, we used the assignR package in R (Ma et al., 2020). This approach employed a semi-parametric Bayesian inversion method. First, we created a tissue-specific wing isoscape by calibrating an interpolated mean annual precipitation map of the US (retrieved from waterisotopes.org) with the relationship of true armyworm δ^2H_w and environmental water:

$$\delta^2H_w = 0.4 \times \delta^2H_{precip} - 84.4$$

and the 13‰ residual SD from the regression (Hobson et al., 2018) using ordinary least squares to fit a linear calibration (Ma et al., 2020). This created two raster objects—the predictive tissue isoscape and a 1σ uncertainty surface. Covariance was estimated by randomly drawing values from the environmental isoscape distribution at each known origin sample location and iteratively fitting the rescaling function (100x), then calculating the covariance of the simulated isoscape and rescaling model residuals. To constrain the isoscape to the known distribution of *E. auxiliaris*, we georeferenced a figure from Burton et al. (1980) depicting the potential range of the moth, created a spatial polygon from the georeferenced figure, and used the spatial polygon to "clip" the isoscape. We opted to use the potential range of the moth (rather than the known range) because the potential range better encompassed the values found in the migrants' stable hydrogen distribution.

To ensure comparability between our data and the isoscape calibrated with the values of Hobson et al (2018), we passed our sample values through the refTrans function to re-calibrate our sample values with values assigned to the EC-01 (δ^2H = -197.0‰) and EC-02 (δ^2H = -54.1‰) standards that Hobson et al. (2018) used to calibrate their samples to VSMOW during their laboratory analysis. We grouped samples according to mountain range, and, within the Absaroka Range, differences established by Tukey's HSD between mountain peaks/years. We then passed our sample values of unknown origin through the pdRaster function, which computed the posterior probability of sample origin for each grid cell within the isoscape. This returned a raster object which contained one probability density surface for each sample. To provide an understanding of moth natal origin for each mountain range, we used the unionP function, which aggregated probabilities from all samples by calculating the probability that any one sample came from each grid cell within the isoscape. This was done by summing the probabilities of all samples and rescaling such that the results summed to unity across the region.

Results

Great Plains samples: Spring and fall migratory period

Spring samples. There was strong evidence that both year and ecoregion had an effect on mean δ^2H_w (ANOVA, $F_{3,1014} = 17.4$, $p < 0.001$ and $F_{4,1014} = 54.2$, $p < 0.001$, respectively). We found very strong evidence for an interaction between year and ecoregion (ANOVA, $F_{7,1014} = 9.6$, $p < 0.001$), and used the flattened year/ecoregion variable to perform post-hoc testing. Broadly, ecoregion δ^2H_w values followed anticipated patterns (per precipitation) given their latitude: the western cordillera had the most negative distributions, the cold deserts had the second-most negative distributions, and the south-central semiarid prairies had the most moderate stable hydrogen distributions (Figure 6). Exceptions to this finding (wherein stable hydrogen distributions were significantly different as compared to other years of collection within the ecoregion) included 2021/south-central semiarid prairies and 2020/west-central semiarid prairies. The most geographically distinct ecoregions—the western cordillera and south-central semiarid prairies—were significantly different for all year combinations excluding western cordillera/2019 and south-central semiarid prairies/2021 (Figure 6).

Fall samples. Although there was strong evidence that both year and ecoregion had an effect on mean δ^2H_w (ANOVA, $F_{1,286} = 27.1$, $p < 0.001$ and $F_{3,286} = 4.5$, $p = 0.004$, respectively), there was little to no evidence that an interaction between year and ecoregion had an effect on δ^2H_w (ANOVA, $F_{1,286} = 1.4$, $p = 0.24$). Using the additive model (δ^2H_w as a function of year + ecoregion), we found significant differences between cold deserts/the western cordillera (Tukey's HSD, $p = 0.009$) and south-central semiarid prairies/the western cordillera (Tukey's HSD, $p = 0.03$). Although patterns found in fall ecoregion δ^2H_w values were less distinctive than those found in the spring, more northern ecoregions tended to have more negative distributions (Figure 7).

Migratory patterns within ecoregions. We grouped and analyzed army cutworm moths according to ecoregion/season and, for established differences, year(s). Due to constraints posed by using only a single stable isotope that varies primarily along a north-south gradient, resolution of the union probability maps produced for ecoregions was not fine enough to elucidate the exact migratory corridors along which migrants traveled on a longitudinal basis. Instead, we used union probability maps generated for ecoregions to assess the migrants' probability of having originated from areas of similar latitude. Of the spring collection, only the south-central semiarid prairies (2018-2020) and west-central semiarid prairies (2020 only) had high probability of origin that fell within their respective ecoregion. The south-central semiarid prairies (2021 only), cold deserts, western cordillera, west-central semiarid prairies (2021 only), conversely, were composed of migrants that had higher probability of northern origin as compared to the latitude of their respective ecoregion. Migrants collected in the western cordillera had the highest probability of origin in the northern extent of the army cutworm moth's potential range across all years (Figure 8), as did the cold deserts.

Returning migrants (fall collection) did not seem to exhibit natal-origin site fidelity. Both the western cordillera and west-central semiarid prairies were again primarily composed of migrants with the highest probability of origin in the northern extent of the moth's potential range. As was seen in the spring migratory period, the cold deserts and south-central semiarid prairies were composed of migrants with likely origins that fell within the bounds of each ecoregion, although high probability was also found north of these ecoregions. For all spring and fall year/ecoregion union probability maps, refer to Figures 1-12 in Appendix B.

Moth aggregation site samples

We found a significant difference in mean δ^2H_w between the Absaroka Range and the Lewis Range (two-sample t-test, $t_{699} = -6.60$, $p < 0.001$). As predicted, stable hydrogen values of moths collected within the Lewis Range were more negative than values of moths collected within the Absaroka Range (Figure 9). Because some moth aggregation sites had such limited sample sizes within the Lewis Range ($n = 5$ or fewer), we did not test for differences in δ^2H_w values between mountain peaks of this area.

Within the Absaroka Range, we established that moths were not primarily coming from the Bighorn Basin (as O'Brien and Lindzey (1994) had posited) because there was no evidence that mean δ^2H_w from moths collected within this region was comparable to the Bighorn Basin's predicted value of -127.8‰ (two-sample t-test, $t_{623} = -0.57$, $p = 0.57$). Instead, across all years and peaks, moth wings of the Absaroka Range had a mean stable hydrogen value of -143.9‰. Stable hydrogen values at the peak/year level had a surprising amount of variation, ranging from a mean of -109.8‰ to -171.9‰ (Table 3; Figure 10), and there was very strong evidence that mean δ^2H_w varied, as compared to other years, for at least one year (ANOVA, $F_{4,614} = 24.8$, $p < 0.001$). This variation suggests that there was limited evidence for a sub-population, as would have been evidenced by distributions that tended to center on one value.

Natal origin. Depictions of natal origin are inherently reflective of the underlying δ^2H_p isoscape from which the tissue-calibrated isoscape was derived. Thus, in the figures depicting union probability, the narrower depiction of origin that is consistently seen along the border of Alberta and British Columbia and the broader "band" of natal origin for regions falling within the Great Plains are both artifacts of patterns in precipitation and, secondarily, the mixing of bodies of water.

To establish the natal origin of moths collected from the Lewis Range in 2019, we pooled δ^2H_w values from all peaks. Moths of this range had high probability of origin exclusively within the northwestern extent of the army cutworm's known range, wherein the vast majority of migrants likely originated in the western half of Canada (Figure 11). Some migrants may have also flown from Montana, Idaho, and Wyoming, but the likelihood that any one sample originated from those areas was substantially lower.

Moths collected from the Absaroka Range were grouped and analyzed on a yearly basis (pooling all sample values from all peaks), as prescribed by the differences found using Tukey's HSD. Across all years of collection, source populations were primarily composed of migrants with the highest likelihood of origin in Canada, followed by Montana, Idaho, and Wyoming (Figs. 10-14). Within Canada, the highest probability of origin was found in the northernmost extent of the moth's range and/or along the border of British Columbia and Alberta for any given year. Moths may have also originated from within all areas of British Columbia, Alberta, and Saskatchewan, although the strength of this probability varied more across years.

Within the United States, likely areas of origin included the western half of Montana, the western half of Wyoming, and the eastern portion of Idaho for all years. Some years, however, were characterized by very diverse origins in addition to patterns found in all years. Moths collected in 2017 had moderate probability of origin in parts of Washington, Oregon, California, Nevada, Utah, and Colorado (Figure 12). In 2020, migrants likely originated from each state within their natal range (Figure 15). The probable origin of migrants collected in both 2019 and 2021 were again constrained primarily to the northwestern extent of their range (Figures 13, 14, and 16).

Our fall armyworm feeding experiment confirmed that wing stable hydrogen values do not change over the course of two weeks of adult feeding. Even when fed heavily deuterated sugar water (844.65 ± 0.43‰), there was no evidence that mean δ^2H_w differed from mean δ^2H_w of moths fed a sugar solution made with tap-water (-138.86 ± 0.09‰) (Wilcoxson rank sum test, W = 50, p = 0.72). Thus, this finding suggests that δ^2H_w values of moths collected from throughout the Great Plains and on mountain peaks were representative of larval feeding habits.

Characterizing natal origin biomes: Absaroka Range. Natal source populations of all moth aggregation sites fed almost exclusively on C3 plants, as each moth aggregation site/year was characterized by a mean δ^{13}Cw value close to, if not exactly, -27‰ (Table 5). Although $\delta^{13}C_w$ values did not vary significantly between peaks (ANOVA, $F_{2,197} = 0.87$, p = 0.42), there were significant differences found between years (ANOVA, $F_{4,197} = 3.81$, p = 0.0053), including: 2017 and 2019, 2019 and 2020, and 2019 and 2021 (Tukey's HSD, p = 0.0013, 0.011, and 0.019, respectively). In 2019, a much larger proportion of moths fed in a C4 habitat as larvae, although this difference may have been inflated due to the limited sample size for that year.

Stable nitrogen values, however, did not vary significantly between years ($F_{4,197} = 1.49$, p = 0.21) or peaks ($F_{2,197} = .92$, p = 0.4), and, for each moth aggregation site and year of collection, mean δ^{15}N ranged from 5.4‰ to 7.3‰ (Table 2). Few moths fed in a heavily fertilized agroecosystem (as distinguished by a $\delta^{15}N_w$ value of ~14‰ or more). Of the three individuals that were likely feeding in a C4 biomes, one of their respective $\delta^{15}N_w$ values was undoubtedly from an agricultural biome (> 15‰), while the remaining two had $\delta^{15}N_w$ values closer to the average.

Discussion

With some exceptions, δ^2H distributions tended to become more negative when moving from southern to northern ecoregions for both spring and fall collection. Significant differences in mean δ^2H_w were found between geographically distinct ecoregions for most spring year/ecoregion combinations, indicating that point of origin influenced (to an extent) migratory pathway. Rather than traveling along latitudinal bands, however, there was surprisingly strong evidence for north-south migration in most ecoregions. Northern ecoregions, including the western cordillera and west-central semiarid prairies, were characterized by migrants that had the highest probability of origin solely in Canada; moderate probability of origin was found throughout the northwestern region of the Great Plains. Southern ecoregions, including one year of collection for the south-central semiarid prairies, all years of collection for the cold deserts, and all years of collection for the warm deserts, were also characterized by migrants with high probability of origin north of each respective ecoregion; however, high probability of origin was also found in the northwestern US. Fall migrants did not show natal origin fidelity, as migrants with likely Canadian origins in the spring often constituted a large proportion of trap catches in northern ecoregions of the Great Plains during the fall.

Similar patterns were found in moths collected from summer ranges. Mean δ^2H_w of the Lewis Range was significantly different (more negative) than the Absaroka Range—i.e., source populations of the more northern range (Lewis) were constituted by migrants of overall more northern origins than the southern range (Absaroka). Migrants collected in the Lewis Range had the highest probability of origin in the northernmost region of the moth's potential range, just along the southern border of the Northwest Territories and below, and along the border of British Columbia and Alberta. A much lower probability of origin was found in Montana, Wyoming, and Idaho, suggesting that most migrants originated from Canada.

Origins of migrants collected in the Absaroka Range were much more varied than we anticipated. Across all years, probability of origin was highest in Canada, Montana, Idaho, and Wyoming; however, migrants collected in years characterized by more diverse stable hydrogen values (including 2017, 2020, and 2021) could have originated from throughout the entire northern third of the moth's potential range. Migrants in 2020 had potential origins that spanned the entirety of the moth's potential range, excluding the most southeastern region (i.e., Texas and Oklahoma). Altogether, there was very limited evidence for a subpopulation, and the hypothesis of O'Brien and Lindzey (1994) that migrants were primarily supplied by the Bighorn Basin has little support.

Stable carbon values of moths collected in the Absaroka Range were overwhelmingly representative of C3 biomes. Excluding three individuals, all randomly sampled army cutworm moths from this range fed on C3 plants during their larval stage. These findings are not altogether unsurprising, even in light of the army cutworm moth's varied larval feeding habits (Burton et al., 1980)—corn and sorghum (cultivated C4 plants) are planted in the late spring, and germination may occur beyond the window of adult moth emergence for some areas (Carter et al., 1989; Kucharik, 2006). This, however, may indicate that moths do not feed as readily on C4 prairie grasses that may be available during their larval stage. Stable nitrogen measurements also indicated that few migrants fed in heavily fertilized agroecosystems, suggesting that there is limited evidence of risk to larval populations due to highly intensive agricultural practices. Of the individuals that fed on corn or sorghum, only one migrant clearly originated from an agroecosystem that was heavily fertilized.

Across summer, spring, and fall collection, year was found to have a significant effect on both moth δ^2H_w and $\delta^{13}C_w$. The significance of year likely alludes to the variety of factors varying on an annual basis that influence moth populations (e.g., regional weather and crop distributions). As was illustrated with natal origin probability that varied year-to-year for the

Absaroka Range, summering ranges in the Rocky Mountains will be “supplied” by an array of natal origin sites that vary yearly, rather than by a subpopulation specific to particular mountain ranges. This finding is also supported by the army cutworm moth’s sporadic nature as a pest; rather than consistently reaching economic outbreak levels within certain locations, outbreaks occur somewhat randomly throughout their natal range (Burton et al., 1980).

The distance army cutworm moths potentially migrate in the spring proposed here is substantial. Measuring from just above the southern border of the Northwest Territories (the highest latitude per high natal origin probability) to the Absaroka Range, army cutworm moths are potentially migrating as far as 1800 km. Comparatively, both the Australian Bogong moth (*Agrotis infusa*) and black cutworm (*Agrotis ipsilon*) undertake a bi-annual migration of as far as 1000 km and weather-assisted migration of as far as 1266 km, respectively (Showers et al., 1989a; Warrant et al., 2016). Without the aid of wind, army cutworm moths have the potential to fly as far as 64 km per night (Koerwitz & Pruess, 1964). Thus, to complete such a migration in the time frame between adult emergence in Canada and the onset of summer in the Rocky Mountains (slightly less than a month), army cutworm moths would likely need to fly above the flight boundary layer and with the aid of preferential winds, as is seen in the aforementioned noctuid migrants (Chapman et al., 2008a; Chapman et al., 2008b; Showers et al., 1989a).

As we mentioned previously, the conclusions that can be drawn using an isoscape based on a stable isotope that varies primarily along a north-south gradient are limited. The resolution and accuracy of the assignments we presented here would be greatly improved with the inclusion of a second isotope, such as carbon, and potentially a trace element (Heinrich & Collins, 2017; Holder et al., 2014). As such, union probability maps, particularly pertaining to longitudinal accuracy, should be treated with caution. For example, there was a high probability that moths flew from either side of the Rocky Mountains to reach summering ranges. Rather than definitively illustrating that moths migrate from either side of the Rocky Mountains, this result could be an artifact of the limitations of stable hydrogen because δ^2H values were almost identical on either side of the Rockies.

Furthermore, values found in moth populations collected during the summer were not fully encompassed by the predictive map; some values were lighter than even the lower range of -150‰ found in the Northwest Territories and along the border of Alberta and British Columbia. Union probability maps generated for collections in which mean δ^2H_w was less than -150‰ may therefore not be accurate. Ground-truthing with moth δ^2H_w captured at point of emergence to establish the accuracy of the predictive map, or to create an army cutworm moth-specific isoscape, would be of substantial use in rectifying this limitation.

A potential explanation for some of the extremely negative values we saw may have resulted from moth wing δ^2H changing with adult feeding. Although wings are more metabolically inert than other insect tissues, these chitinous structures contain veins through which hemolymph is pumped, and therefore hydrogen ratios from wings may be representative of a mixture of larval and adult food sources. However, this is unlikely because our two-week feeding study with fall armyworm indicated that moth δ^2H_w values did not drift, even when moths were fed heavily deuterated sugar water. Because the army cutworm moth is such a long-lived migrant, future studies should document whether this conclusion holds true over a longer period.

Ultimately, given the varied moth wing δ^2H values of migrants we collected from the Absaroka and Lewis ranges, there was very strong evidence that army cutworm moth aggregation sites are not supplied by a subpopulation. Thus, moth populations at mountain peaks are likely insulated against regional moth population declines in their natal range, and moth availability at moth aggregation sites should not vary drastically year to year. Rather than traveling along a latitudinal band, as we had hypothesized, moths collected in these ranges had the highest probability of origin in Alberta and British Columbia, followed by Montana, Wyoming, and Idaho. Interestingly, there was also strong evidence that migrants collected from throughout the Great Plains often originated from areas north of the ecoregion in which they were collected. Altogether, our paper establishes that moth aggregation sites are likely "supplied" by a geographical array of natal origin sites and provides the first evidence that army cutworm moths may migrate northwest to southeast, in addition to previously documented east-west movement.

Table 1: Summary of $\delta^{2}\mathrm{H}_{\mathrm{w}}$ data for army cutworm moths, *Euxoa auxiliaris*, collected during the spring emergence period within the Great Plains (2018-2021, n = 1031).

δ^{2}H (‰ VSMOW**)				
Year	Ecoregion	*n*	Mean ± SD	95% CI
2018	Cold deserts	6	-150.7 ± 25.2	-177.2 – -124.3
2019	Cold deserts	108	-127.9 ± 21.3	-131.9 – -123.8
2020	Cold deserts	161	-132.1 ± 22.3	-135.6 – -128.7
2021	Cold deserts	33	-122.8 ± 27.4	-132.6 – -112.9
2018	Western cordillera	4	-166.3 ± 2.0	-169.5 – -163.1
2019	Western cordillera	18	-142.6 ± 23.6	-154.3 – -130.9
2020	Western cordillera	62	-145.1 ± 20.5	-150.3 – 139.9
2021	Western cordillera	16	-159.2 ± 14.8	-167.1 – -151.3
2018	SC semiarid prairies*	45	-118.7 ± 15.7	-123.5 – -114.0
2019	SC semiarid prairies	67	-116.5 ± 19.9	-121.4 – -111.7
2020	SC semiarid prairies	177	-119.1 ± 12.3	-120.9 – -117.3
2021	SC semiarid prairies	103	-130.8 ± 13.0	-120.9 – -117.3
2020	Warm deserts	22	-130.6 ± 10.5	-133.4 – -128.3
2020	WC semiarid prairies^{+}	189	-130.8 ± 12.3	-132.6 – -129.0
2021	WC semiarid prairies	20	-159.5 ± 19.8	-168.8 – -150.2

**Vienna Mean Standard Oceanic Water

*South central semiarid prairies

$^{+}$Western central semiarid prairies

Table 2: Summary of $\delta^{2}\mathrm{H}_{\mathrm{w}}$ for army cutworm moths collected during the fall migratory period within the Great Plains (2020-2021, n = 293).

δ^{2}H (‰ VSMOW**)				
Year	Ecoregion	*n*	Mean ± SD	95% CI
2020	Cold deserts	38	-122.4 ± 13.9	-127.0 – -117.8
2020	Western cordillera	49	-133.9 ± 19.4	-139.5 – -128.3
2021	Western cordillera	14	-154.9 ± 25.9	-169.8 – -139.9
2020	SC semiarid prairies	46	-124.6 ± 20.6	-130.7 – -118.5
2020	WC semiarid prairies^{+}	85	-132.3 ± 19.6	-136.5 – -128.0
2021	WC semiarid prairies	61	-145.3 ± 19.7	-150.4 – -140.2

**Vienna Mean Standard Oceanic Water

$^{+}$Western central semiarid prairies

Table 3: Summary of δ^{2}H$_{w}$ data for army cutworm moths collected each summer at mountain peaks within the Absaroka Range (2017-2021, $n = 618$).

δ^{2}H (‰ VSMOW**)				
Year	Location	*n*	Mean ± SD	95% CI
2017	A	89	-153.8 ± 23.2	-158.7 – -149.0
2018	A	271	-135.6 ± 30.6	-139.3 – -132.0
2020	A	34	-134.6 ± 21.7	-142.2 – -127.0
2021	A	50	-153.2 ± 22.6	-159.6– -146.8
2018	B	7	-109.8 ± 23.0	-131.0 – -88.6
2020	B	11	-139.8 ±14.7	-149.6 – -129.9
2021	B	50	-155.5 ± 18.4	-160.8 – -150.3
2019	C	20	-171.9 ± 30.3	-186.1 – -157.8
2020	C	42	-132.2 ± 19.6	-138.4 – -126.1
2021	C	50	-160.3 ± 19.3	-165.8 – -154.8

**Vienna Mean Standard Oceanic Water

Table 4: Summary of δ^{2}H$_{w}$ data for army cutworm moths collected during the summer of 2019 within the Lewis Range (2019, $n = 77$).

δ^{2}H (‰ VSMOW**)				
Year	Location	*n*	Mean ± SD	95% CI
2019	D	30	-145.5 ± 25.6	-155.0 – -135.9
2019	E	13	-197.0 ± 43.1	-223.0 – -171.0
2019	F	13	-178.8 ± 36.2	-200.7 – -156.9
2019	G	2	-158.9 ± 18.2	NA
2019	H	3	-170.9 ± 11.9	-200.5 – -141.4
2019	I	2	-179.3 ± 0.4	NA
2019	J	14	-174.0 ± 33.1	-193.1 – -154.9

**Vienna Mean Standard Oceanic Water

Table 5: Summary of δ^{13}C$_{w}$ data for army cutworm moths collected each summer at mountain peaks within the Absaroka Range (2017-2021, $n = 205$).

δ^{13}C (‰ VPDB^{1})				
Year	Location	*n*	Mean ± SD	95% CI
2020	B	6	-27.0 ± 0.8	-27.9 – -26.1
2021	B	33	-26.7 ± 2.3	-27.5 – -25.9
2017	A	29	-27.6 ± 1.4	-28.2 – -27.1
2018	A	29	-26.7 ± 1.2	-27.2 – -26.3

Table 5 Continued

Year	Location	*n*	Mean ± SD	95% CI
2020	A	25	-27.3 ± 1.3	-27.8 – -26.8
2019	C	17	-27.0 ± 3.7	-27.5 – -23.7
2020	C	23	-27.0 ± 1.0	-27.4 – -26.6
2021	C	43	-27.2 ± 1.0	-27.5 – -26.9

[1]Vienna Peedee Belemnite

Table 6: Summary of $\delta^{15}N_w$ data for army cutworm moths collected each summer at mountain peaks within the Absaroka Range (2017-2021, *n* = 205).

δ^{15}N (‰ VPDB[1])				
Year	Location	*n*	Mean ± SD	95% CI
2020	B	6	5.4 ± 1.4	3.9 – 6.8
2021	B	33	6.1 ± 3.1	5.0 – 7.2
2017	A	29	6.4 ± 3.5	5.1 – 7.7
2018	A	29	5.7 ± 2.8	4.7 – 6.8
2020	A	25	6.2 ± 3.4	4.8 – 7.6
2019	C	17	7.3 ± 3.8	5.3 – 9.2
2020	C	23	5.3 ± 2.5	4.2 – 6.3
2021	C	43	6.7 ± 2.6	5.9 – 7.5

[1]Vienna Peedee Belemnite

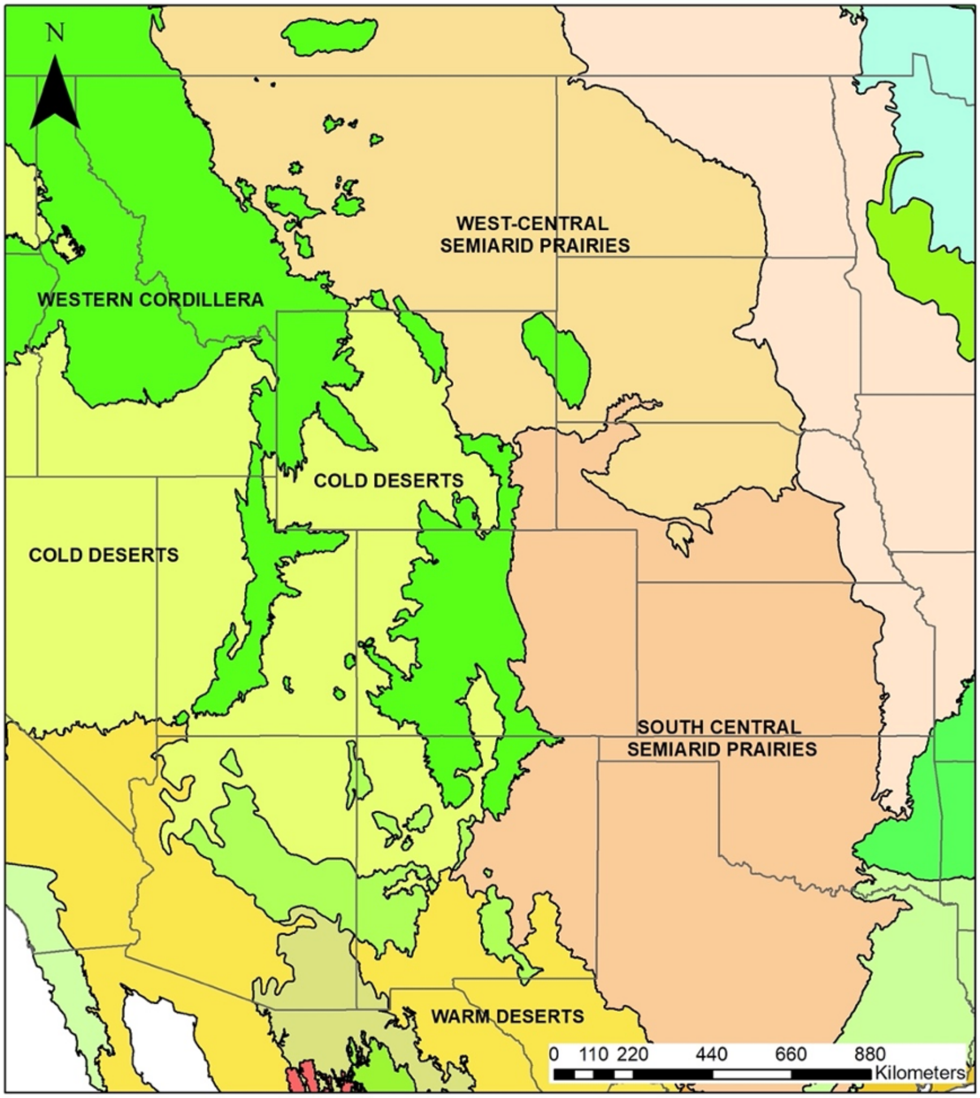


Figure 3: The ecoregions used to delineate the groupings of spring and fall army cutworm moth, *Euxoa auxiliaris*, samples, including the west-central semiarid prairies, south central semiarid prairies, cold deserts, and western cordillera (EPA, 2022). Only labeled ecoregions were used to group samples.

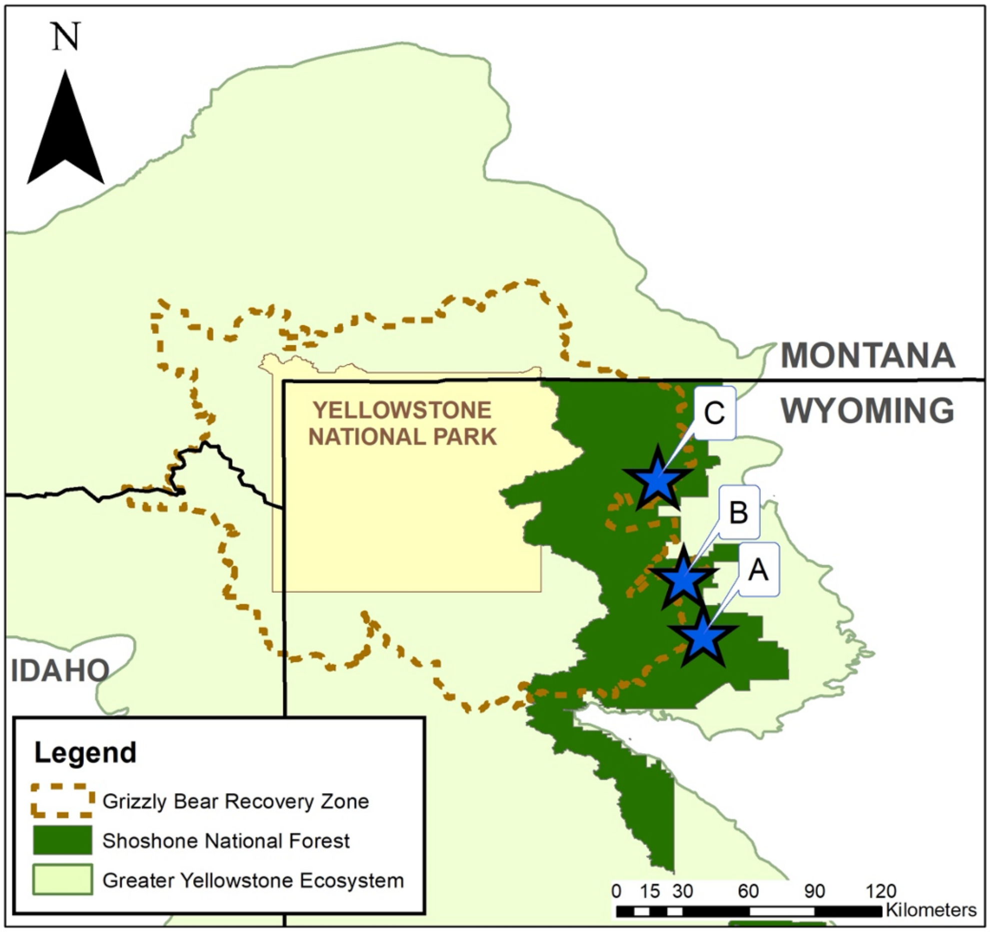


Figure 4: Army cutworm moth summer collection sites A-C located in the Absaroka Mountain Range (2017-2021).

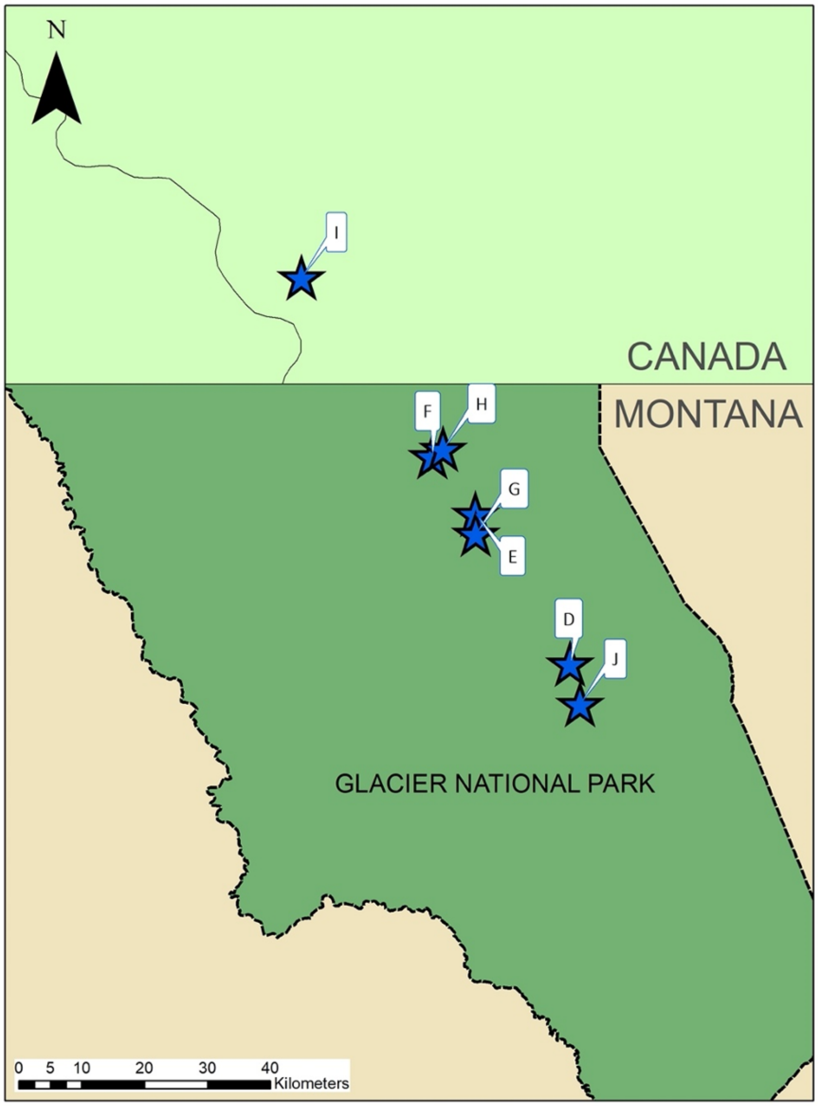


Figure 5: Summer collection sites (I-J) in the Lewis Mountain Range (2019).

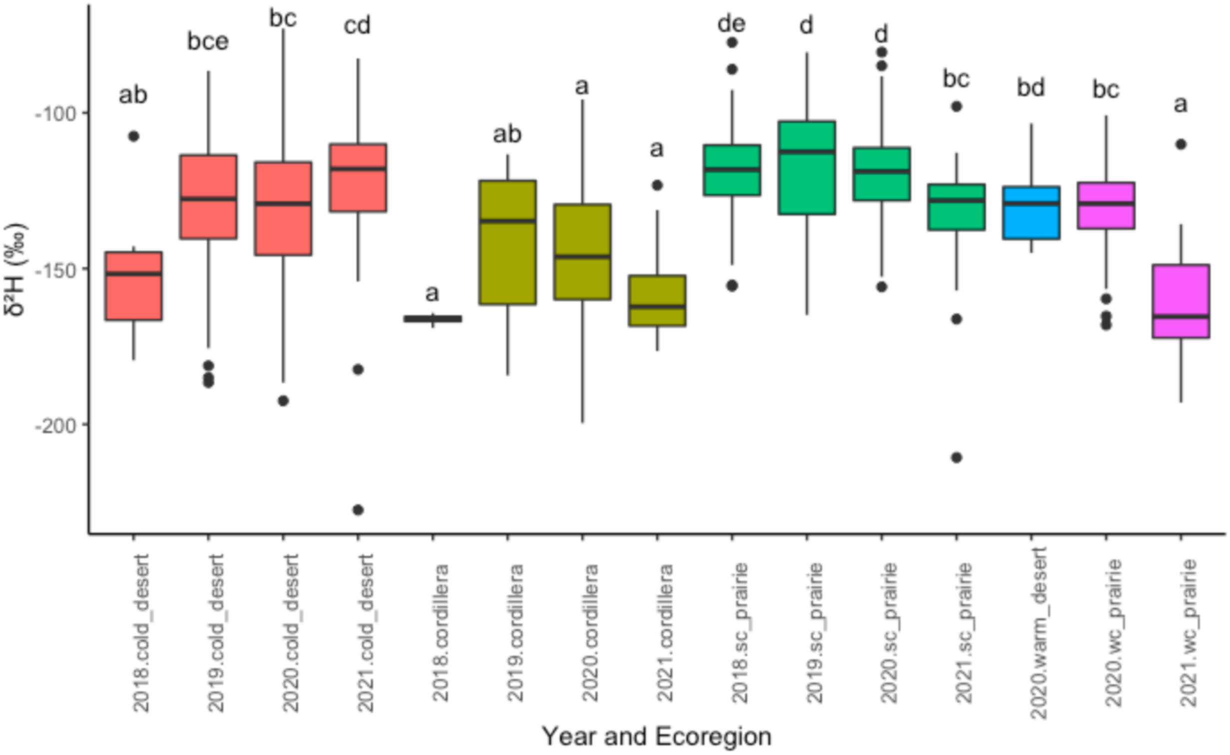


Figure 6: Stable hydrogen distribution of army cutworm moths (*Euxoa auxiliaris*) grouped per ecoregion in which they were collected and the year of collection during the spring. A boxplot with no letter in common indicates that the mean of its respective flattened peak/year variable is significantly different (Tukey's LSD, α = 0.05). See Table 1 for sample sizes.

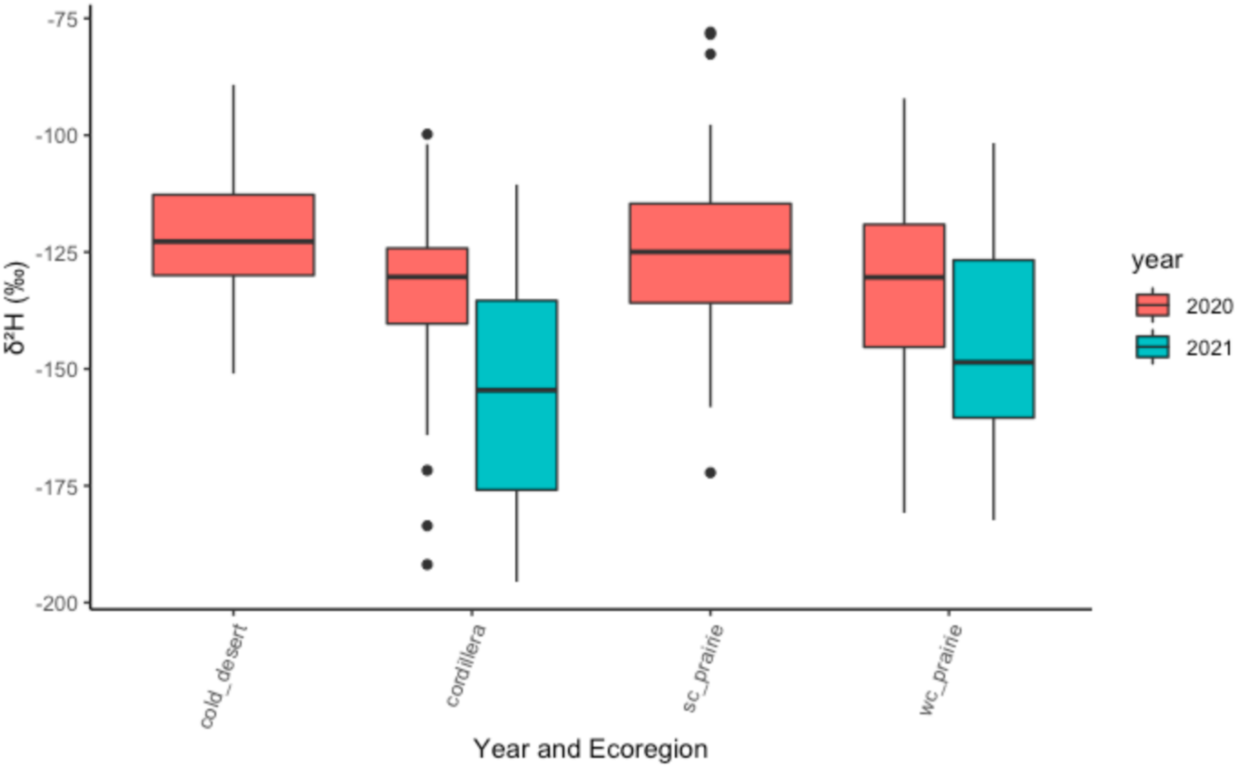


Figure 7: Stable hydrogen distribution of army cutworm moths (*Euxoa auxiliaris*) grouped per ecoregion in which they were collected and the year of collection during the fall. See Table 2 for sample sizes.

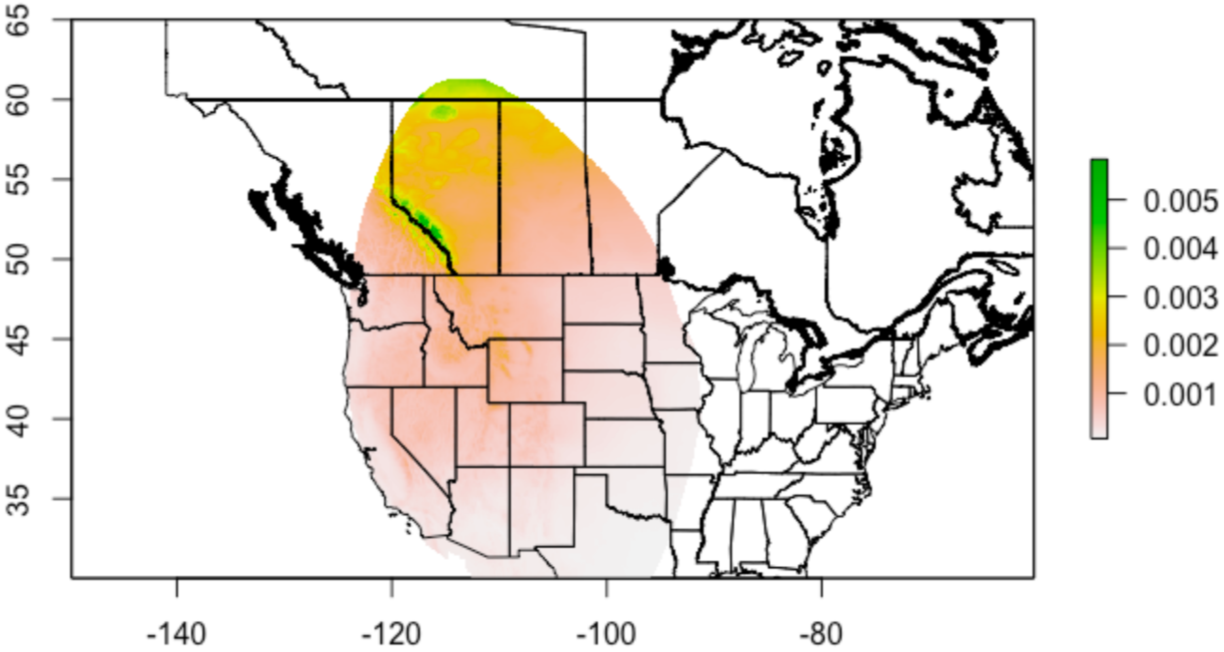


Figure 8: Union probability, the probability that any army cutworm moth (*Euxoa auxiliaris*) from the group originated from any cell within the army cutworm moth's known range, calculated for the western cordillera in the spring of 2018, 2019, and 2021 (*n* = 100). Probability of origin is illustrated on the right, moving from lower probability of origin (pink) to highest probability of origin (green). The x-axis illustrates longitude, and the y-axis illustrates latitude (decimal degrees).

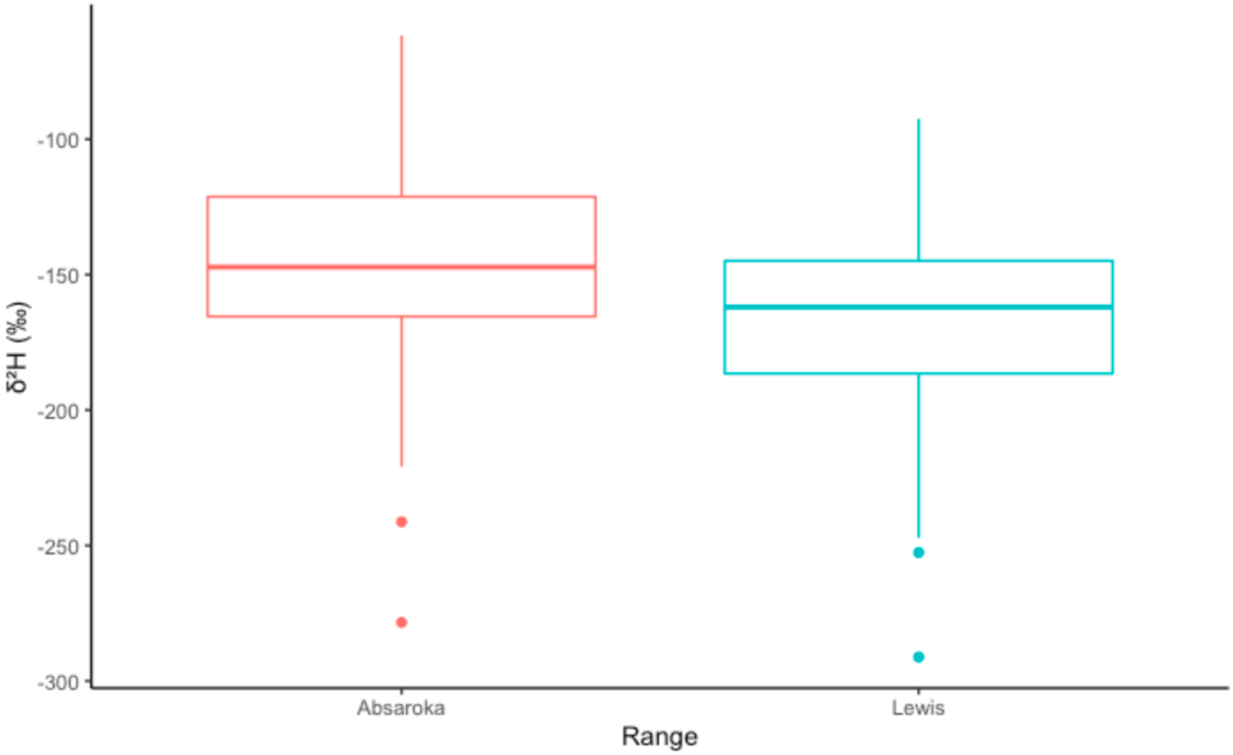


Figure 9: Boxplots of δ^2H_w values of army cutworm moths, *Euxoa auxiliaris*, collected from the Lewis Range and the Absaroka Range.

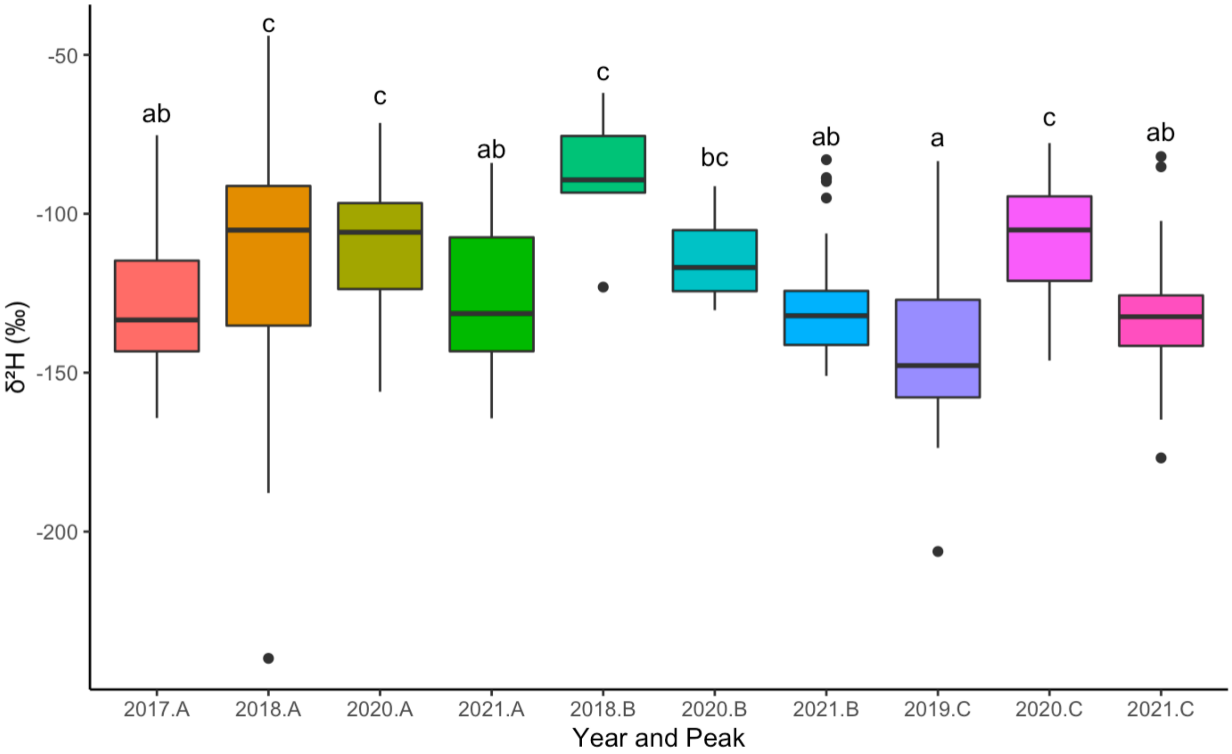


Figure 10: Stable hydrogen distribution of army cutworm moths, *Euxoa auxiliaris*, collected within the Absaroka Range during the summer, grouped according to both the peak and year of collection—"YYYY.Peak" (2017-2021). A boxplot with no letter in common indicates that the mean of its respective flattened peak/year variable is significantly different (Tukey's LSD, α = 0.05). See Table 3 for sample sizes.

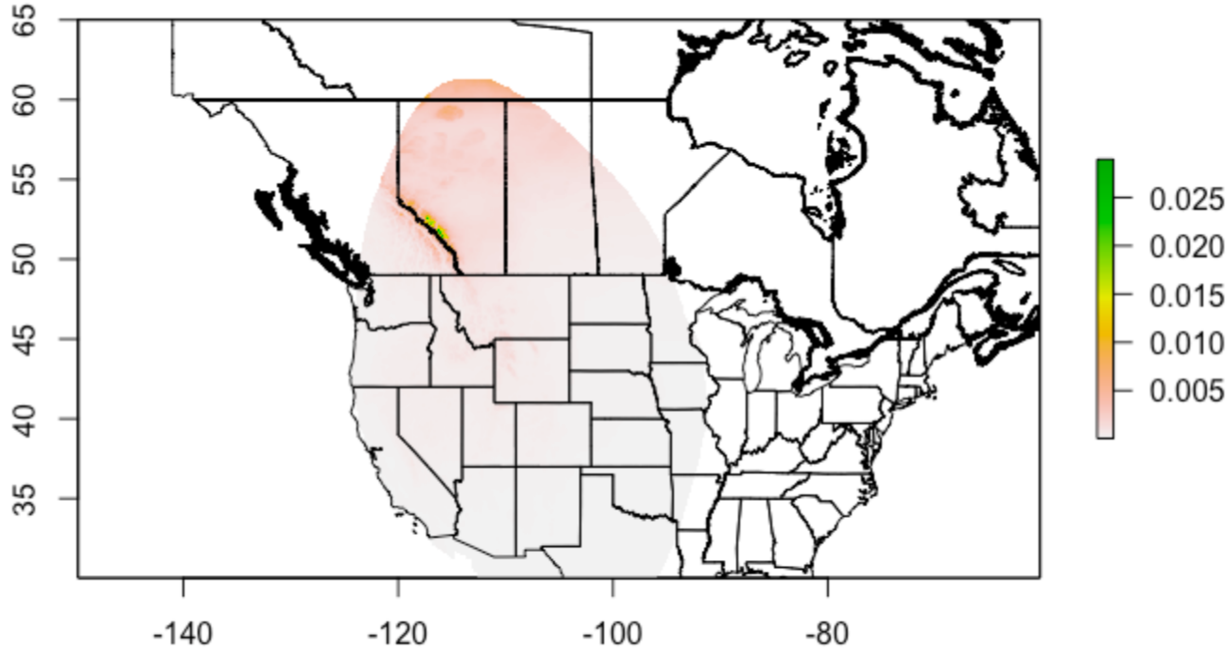


Figure 11: Union probability calculated for army cutworm moths, *Euxoa auxiliaris*, collected in the Lewis Range (2019; *n* = 77).

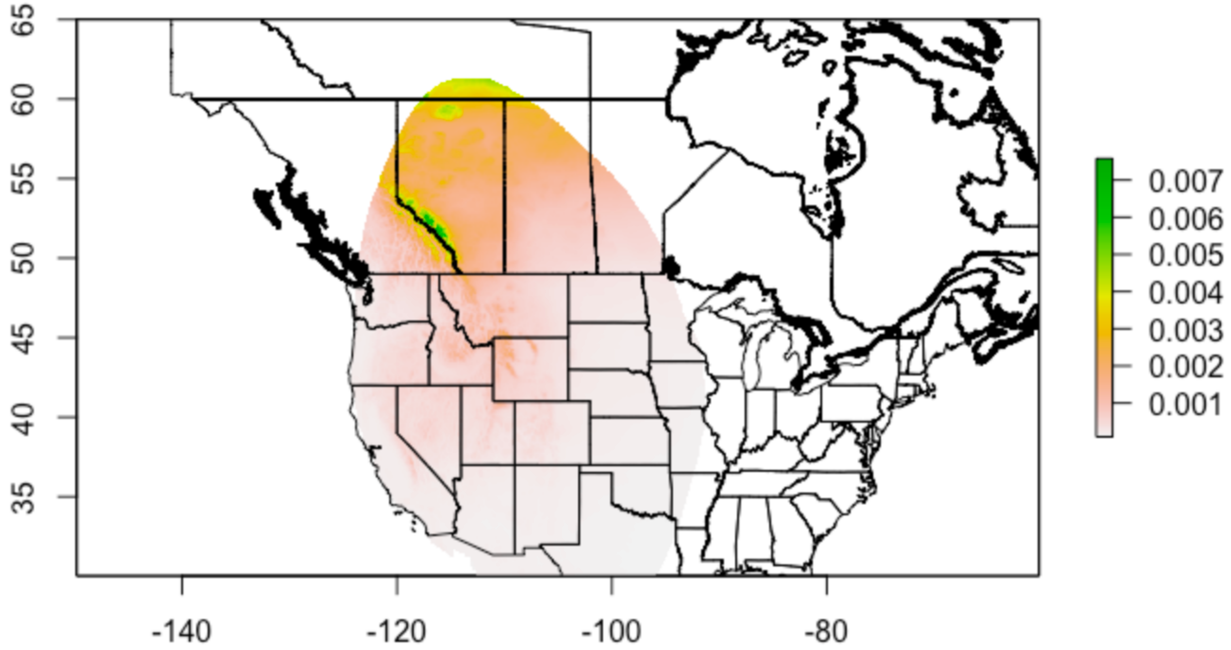


Figure 12: Union probability calculated for army cutworm moths, *Euxoa auxiliaris*, collected from Peak A in the Absaroka Range, 2017 (*n* = 79; Peak A).

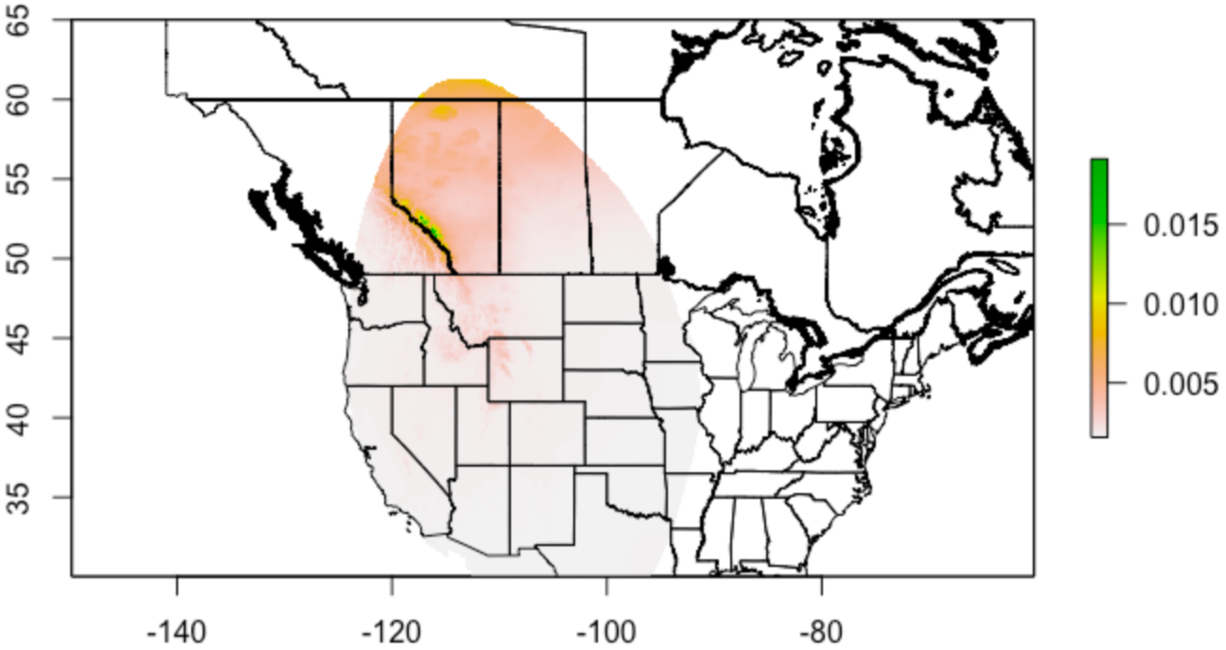


Figure 13: Union probability calculated for army cutworm moths, *Euxoa auxiliaris*, collected from Peaks A and B of the Absaroka Range, 2018 (*n* = 278).

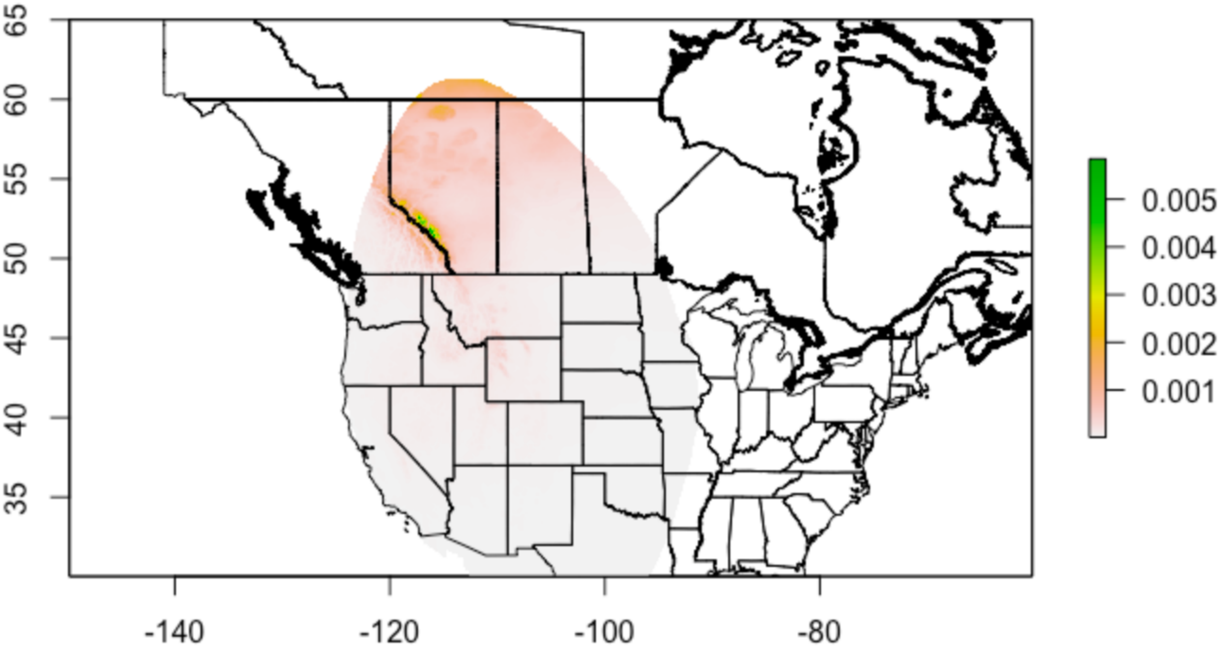


Figure 14: Union probability calculated for army cutworm moths, *Euxoa auxiliaris*, collected from Peak C in the Absaroka Range, 2019 (*n* = 20).

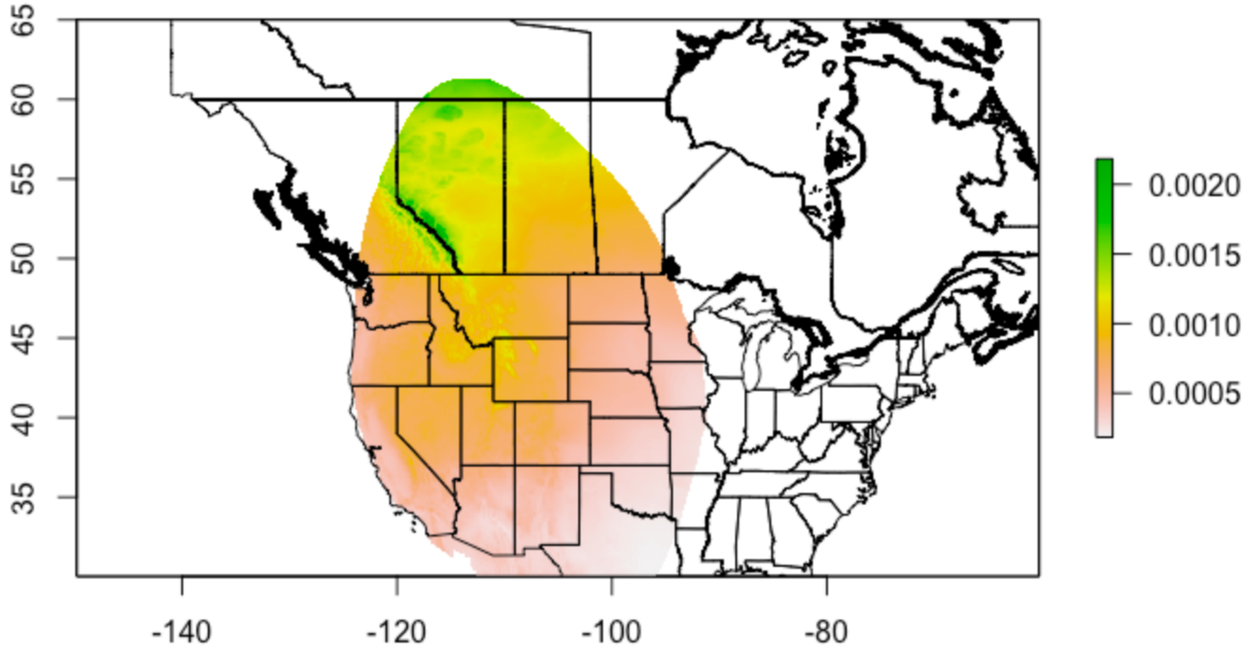


Figure 15: Union probability calculated for army cutworm moths, *Euxoa auxiliaris*, collected from Peaks A, B, and C in the Absaroka Range, 2020 (*n* = 87).

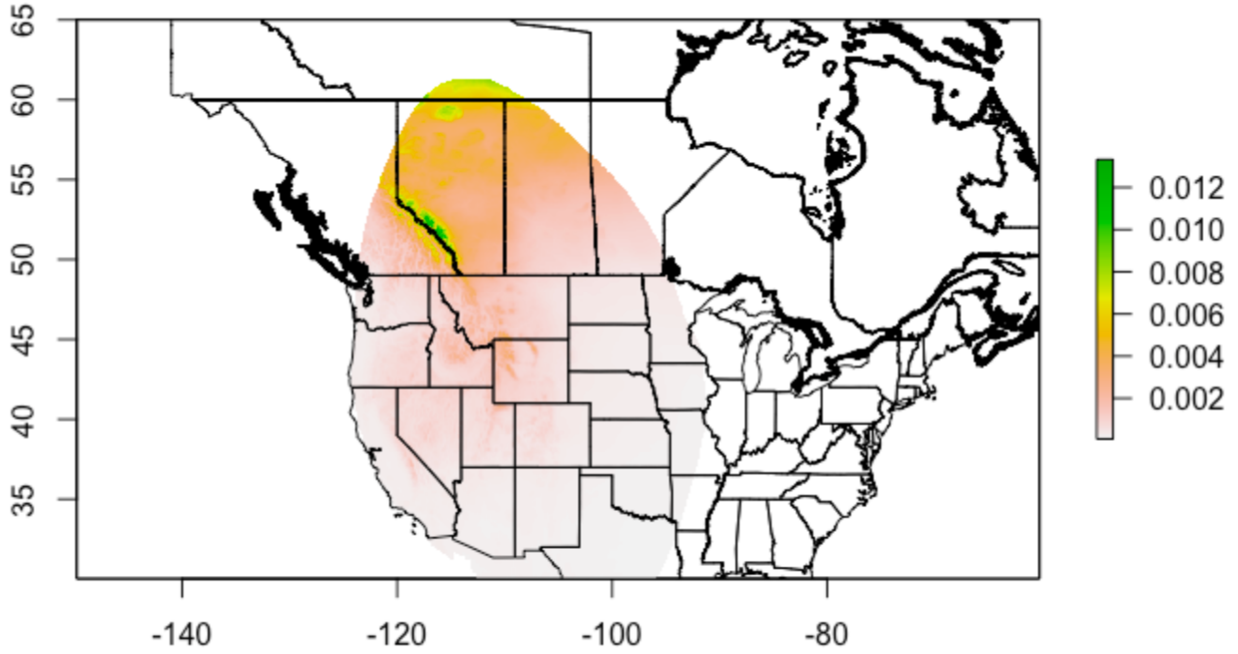


Figure 16: Union probability calculated for army cutworm moths, *Euxoa auxiliaris*, collected from Peaks A, B, and C in the Absaroka Range, 2021 (*n* = 150).

REFERENCES CITED

Augustine, D., Davidson, A., Dickinson, K., & Van Pelt, B. (2021). Thinking like a grassland: Challenges and opportunities for biodiversity conservation in the Great Plains of North America. *Rangeland Ecology & Management, 78*, 281-295.

Baker, F. S. (1944). Mountain climates of the western United States. *Ecological Monographs, 14*(2), 223-254.

Basara, J. B., Maybourn, J. N., Peirano, C. M., Tate, J. E., Brown, P. J., Hoey, J. D., & Smith, B. R. (2013). Drought and associated impacts in the Great Plains of the United States—A review.

Bowen, G. J., Wassenaar, L. I., & Hobson, K. A. (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia, 143*(3), 337-348.

Brattström, O., Bensch, S., Wassenaar, L. I., Hobson, K. A., & Åkesson, S. (2010). Understanding the migration ecology of European red admirals Vanessa atalanta using stable hydrogen isotopes. *Ecography, 33*(4), 720-729.

Burton, R. L., Starks, K., & Peters, D. (1980). The Army Cutworm. *Oklahoma Agricultural Experiment Station*(Bulletin No. B749).

Carter, P. R., Hicks, D. R., Oplinger, E. S., Doll, J. D., Bundy, L. G., Schuler, R. T., & Holmes, B. J. (1989). Grain Sorghum (Milo). *Alternative Field Crops Manual.*

Chapman, J. A., Romer, J. I., & Stark, J. (1955). Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology, 36*(1), 156-158.

Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology, 18*(19), R908-R909.

Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology, 18*(7), 514-518.

Choate, C. M. (1963). *Ordination of the Alpine plant communities at Logan Pass Glacier National Park Montana* Montana State University].

Common, I. (1954). A study of the ecology of the adult bogong moth, Agrotis infusa (Boisd)(Lepidoptera: Noctuidae), with special reference to its behaviour during migration and aestivation. *Australian journal of zoology, 2*(2), 223-263.

Damm, C. (2001). *A Phytosociological Study of Glacier National Park, Montana, U.S.A., with Notes on the Syntaxonomy of Alpine Vegetation in Western North America* Georg-August-Universität zu Göttingen].

Dirks, R. A., & Martner, B. E. (1982). *The climate of Yellowstone and Grand Teton National Parks*. US Department of the Interior, National Park Service.

Endler, J. A. (1973). Gene flow and population differentiation. *Science, 179*, 243-250.

Finklin, A. I. (1986). *A Climatic Handbook for Glacier National Park: With Data for Waterton Lakes National Park* (Vol. 204). US Department of Agriculture, Forest Service, Intermountain Research Station.

Flockhart, D. T., Brower, L. P., Ramirez, M. I., Hobson, K. A., Wassenaar, L. I., Altizer, S., & Norris, D. R. (2017). Regional climate on the breeding grounds predicts variation in the natal origin of monarch butterflies overwintering in Mexico over 38 years. *Global change biology, 23*(7), 2565-2576.

Flockhart, D. T., Wassenaar, L. I., Martin, T. G., Hobson, K. A., Wunder, M. B., & Norris, D. R. (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceedings of the Royal Society B: Biological Sciences, 280*(1768), 20131087.

Fortin, J. K., Schwartz, C. C., Gunther, K. A., Teisberg, J. E., Haroldson, M. A., Evans, M. A., & Robbins, C. T. (2013). Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of Wildlife Management, 77*(2), 270-281.

French, S. P., French, M. G., & Knight, R. R. (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

Hardwick, D., & Lefkovitch, L. (1971). Physical and biotic factors affecting Euxoa species abundance in western North America: a regression analysis. *The Canadian Entomologist, 103*(9), 1217-1235.

Heinrich, K., & Collins, L. (2017). Determining the geographical origin of Asian longhorn beetle (Anoplophora glabripennis) specimens using stable isotope and trace element analyses. *Pest management science, 73*(5), 967-975.

Hobson, K. A., Doward, K., Kardynal, K. J., & McNeil, J. N. (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.

Hobson, K. A., Kusack, J. W., Gootgarts, J., Longstaffe, F. J., & McNeil, J. N. (2022). Using stable isotopes (δ 2H, δ 13C) to identify natal origins and larval host plant use by western bean cutworm, Striacosta albicosta (Lepidoptera: Noctuidae) captured in southern Ontario. *Ecological Entomology*.

Hobson, K. A., Soto, D. X., Paulson, D. R., Wassenaar, L. I., & Matthews, J. H. (2012). A dragonfly (δ2H) isoscape for North America: a new tool for determining natal origins of migratory aquatic emergent insects. *Methods in ecology and evolution, 3*(4), 766-772.

Hobson, K. A., & Wassenaar, L. I. (2019). *Tracking animal migration with stable isotopes*. Academic Press.

Holder, P. W., Armstrong, K., Van Hale, R., Millet, M.-A., Frew, R., Clough, T. J., & Baker, J. A. (2014). Isotopes and trace elements as natal origin markers of Helicoverpa armigera–an experimental model for biosecurity pests. *PloS one, 9*(3), e92384.

Hyodo, F. (2015). Use of stable carbon and nitrogen isotopes in insect trophic ecology. *Entomological Science, 18*(3), 295-312.

Jacobson, L. A., & Blakeley, P. E. (1959). Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America, 52*(1), 100-105.

Kendall, D. M., Kevan, P. G., & LaFontaine, J. D. (1981). Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist, 113*(7), 607-614.

Kevan, P. G., & Kendall, D. M. (1997, 1997/11/01). 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://doi.org/10.1080/00040851.1997.12003268

Koel, T. M., Bigelow, P. E., Doepke, P. D., Ertel, B. D., & Mahony, D. L. (2005). Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries, 30*(11), 10-19.

Koerwitz, F., & Pruess, K. (1964). Migratory potential of the army cutworm. *Journal of the Kansas Entomological Society, 37*(3), 234-239.

Kucharik, C. J. (2006). A multidecadal trend of earlier corn planting in the central USA. *Agronomy Journal, 98*(6), 1544-1550.

Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., Kruk, M. C., Thomas, D., Shulski, M., & Umphlett, N. A. (2013). Regional climate trends and scenarios for the US National Climate Assessment Part 4. Climate of the US Great Plains.

Lafontaine, J. (1987). *The Moths of North America North of Mexico. Fascicle 27.2. Noctuoidea Noctuidae (Part)*. The Wedge Entomological Foundation Washington.

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., & Yeager, L. A. (2012). Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological reviews, 87*(3), 545-562.

Ma, C., Vander Zanden, H. B., Wunder, M. B., & Bowen, G. J. (2020). assignR: An r package for isotope-based geographic assignment. *Methods in ecology and evolution, 11*(8), 996-1001.

Manen, F. T. v., Haroldson, M. A., Bjornlie, D. D., Erbinger, M. R., Thompson, D. J., Costello, C. M., & White, G. C. (2016). Density Dependence, Whitebark Pine, and Vital Rates of Grizzly Bears. *The Journal of Wildlife Management, 80*(2), 300-313.

Marston, R. A., & Anderson, J. E. (1991). Watersheds and vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology, 5*(3), 338-346.

Mattson, D. J., Gillin, C. M., Benson, S. A., & Knight, R. R. (1991). Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology, 69*(9), 2430-2435.

McNabb, D. M., Halaj, J., & Wise, D. H. (2001). Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. *Pedobiologia, 45*(4), 289-297.

Nelson, R. A., Folk Jr, G. E., Pfeiffer, E. W., Craighead, J. J., Jonkel, C. J., & Steiger, D. L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management*, 284-290.

Nunlist, E. (2020). *Grizzly Bears and Humans at Two Moth Aggregation Sites in Wyoming.* Montana State University].

O'Brien, S. L., & 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.

Oku, T., Chiba, T., & Fuse, H. (1983). Phenology and behaviour of cutworms, *Euxoa sibirica* Boisduval and *E. oberthueri* Butler (Lepidoptera, Noctuidae), in Tohoku district: II. Seasonal trap catches of adults in relation to aestival diapause and migration. *Kontyû, 51*, 144-157.

Oku, T., Saito, O., Fuse, H., & Chiba, T. (1982). Phenology and behavior of cutowrms, *Euxoa sibirica* Boisduval and *E. oberthueri* Buter (Lepidoptera, Noctuidae), in Tohoku district: I. Seasonal trap cataches of adults in relation to aestival diapause and migration. *Kontyû, 50*, 301-313.

Omernik, J. M., & Griffith, G. E. (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environmental management, 54*(6), 1249-1266.

Pardo, L. H., & Nadelhoffer, K. J. (2010). Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. In *Isoscapes* (pp. 221-249). Springer.

Pogue, M. G., & Simmons, R. B. (2008). A new pest species of Copitarsia (Lepidoptera: Noctuidae) from the neotropical region feeding on Asparagus and cut flowers. *Annals of the Entomological Society of America, 101*(4), 743-762.

Ponsard, S., Bethenod, M.-T., Bontemps, A., Pélozuelo, L., Souqual, M.-C., & Bourguet, D. (2004). Carbon stable isotopes: a tool for studying the mating, oviposition, and spatial distribution of races of European corn borer, Ostrinia nubilalis, among host plants in the field. *Canadian Journal of Zoology, 82*(7), 1177-1185.

Prasifka, J., & Heinz, K. (2004). The use of C3 and C4 plants to study natural enemy movement and ecology, and its application to pest management. *International Journal of Pest Management, 50*(3), 177-181.

Pruess, K. P., & Pruess, N. C. (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.

Quinby, B. M., Creighton, J. C., & Flaherty, E. A. (2020). Stable isotope ecology in insects: a review. *Ecological Entomology, 45*(6), 1231-1246.

Robinson, E. B., & Dietz, J. L. (2020). *Great Plains*. https://www.britannica.com/place/Great-Plains

Robison, H. L. (2009). *Relationships between Army Cutworm Moths and Grizzly Bear Conservation* University of Nevada, Reno].

Rosenberg, N. J. (1987). Climate of the Great Plains region of the United States. *Great Plains Quarterly*, 22-32.

Schwartz, C. C., Fortin, J. K., Teisberg, J. E., Haroldson, M. A., Servheen, C., Robbins, C. T., & Van Manen, F. T. (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.

Seamans, H. (1928). Forecasting Outbreaks of the Army Cutworm (Chorizagrotis auxiliaris, Grote). *Annual Report of the Entomological Society of Ontario, 58*, 76-85.

Showers, W. B., Smelser, R. B., Keaster, A. J., Whitford, F., Robinson, J. F., Lopez, J. D., & Taylor, S. E. (1989a). Recapture of marked black cutworm (Lepidoptera: Noctuidae) males after long-range transport. *Environmental entomology, 18*(3), 447-458.

Strickland, E. H. (1916). *The Army Cutworm: Euxoa (Chorizagrotis) Auxiliaris Grote* (Vol. Bulletin 13). Canadian Department of Agricultural Entomology.

Sundell, K. A. (1993). *Geology of Wyoming: Geological Survey of Wyoming Memoir No. 5*.

Team, R. C. (2020). *R: A language and environment for statistical computing.* In R Foundation for Statistical Computing. https://www.R-project.org/

Thilenius, J. F., & Smith, D. R. (1985). Vegetation and soils of an alpine range in the Absaroka Mountains, Wyoming. *US Dept of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station*, 1-23.

Triplehorn, C. A., Johnson, N. F., & Borror, D. J. (2005). *Borror and DeLong's Introduction to the Study of Insects*.

USDA. (2022). *United States — Crop Production Maps*. https://ipad.fas.usda.gov/rssiws/al/us_cropprod.aspx

Waddington, J. C., & Wright, H. (1974). Late Quaternary Vegetational Changes on the East Side of Yellowstone Park, Wyoming1. *Quaternary Research, 4*(2), 175-184.

Walkden, H. H. (1950). *Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains*.

Warrant, E., Frost, B., Green, K., Mouritsen, H., Dreyer, D., Adden, A., Brauburger, K., & Heinze, S. (2016). The Australian Bogong moth Agrotis infusa: a long-distance nocturnal navigator. *Frontiers in Behavioral Neuroscience, 10*, 77.

Wassenaar, L. (2009). *Manual for the Use of Stable Isotopes in Entomology*. International Atomic Energy Agency.

Wassenaar, L. I., & Hobson, K. A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences, 95*(26), 15436-15439.

Wassenaar, L. I., & Hobson, K. A. (2000). Improved method for determining the stable-hydrogen isotopic composition (dD) of complex organic materials of environmental interest. *Environmental Science and Technology, 34*, 2354-2360.

Wassenaar, L. I., & Hobson, K. A. (2003). Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopic in Environmental and Health Studies, 39*.

West, J. B., Bowen, G. J., Cerling, T. E., & Ehleringer, J. R. (2006). Stable isotopes as one of nature's ecological recorders. *Trends in Ecology & Evolution, 21*(7), 408-414.

West, J. B., Bowen, G. J., Dawson, T. E., & Tu, K. P. (2009). *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer.

White, D. D. (1996). *Two grizzly bear studies: moth feeding ecology and male reproductive biology* [PhD, Montana State University-Bozeman, College of Letters & Science].

White, D. D. K., K.C..; and Picton, H.D. (1999). Potential Energetic Effects of Mountain Climbers on Foraging Grizzly Bears. *Wildlife Society Bulletin (1973-2006), 27*, 146-151.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998a). Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology, 76*(2), 221-227.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998b). Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology, 76*(5), 835-842.

Willis, B. (1902). Stratigraphy and structure, Lewis and Livingston ranges, Montana. *Bulletin of the Geological Society of America, 13*(1), 305-352.

Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In *Isoscapes* (pp. 251-270). Springer.

Yang, L. H., Ostrovsky, D., Rogers, M. C., & Welker, J. M. (2016). Intra-population variation in the natal origins and wing morphology of overwintering western monarch butterflies Danaus plexippus. *Ecography, 39*(10), 998-1007.

CHAPTER THREE

USING RADAR TO MONITOR MIGRATING ARMY CUTWORM MOTHS, *EUXOA AUXILIARIS*, IN THE ABSAROKA MOUNTAIN RANGE

Abstract

As the availability of grizzly bear (*Ursus arctos horribilis*) food sources continue to shift within the Greater Yellowstone Ecosystem (GYE), understanding of their ecology must improve to address, and, where possible, mitigate the potential consequences of these changes. Among these food sources is the calorically dense army cutworm moth (*Euxoa auxiliaris*), a migratory noctuid that undergoes a remarkable journey from the Great Plains to the Rocky Mountains in the early summer and returns to the plains in the fall. These ephemeral visitors, which migrate to high-elevation aggregation sites, constitute a significant portion of grizzly bears' diets within the GYE. Although long-term monitoring programs have been established for other grizzly bear food sources (e.g., whitebark pine), a monitoring program for the army cutworm moth at moth aggregation sites has not been established, and our understanding of moth abundance at these sites is extremely limited. As such, management of these sites has thus been difficult. To determine whether it would be viable to estimate army cutworm moth abundance with radar, we sampled the airspace ~1 km from a known moth aggregation site with a transportable radar unit during the timeframe preceding peak moth abundance in 2020 and 2021. To verify the identification of the migrants detected, we gathered circumstantial evidence of moth presence in the airspace and examined differences between the diurnal and nocturnal sampling period. From the radar's observations, we determined that approximately 5 million moths had passed through

our 3-km wide sampling plane over a sampling period of 20 hours, estimated the mean direction, and estimated mean speed of the detected targets. Based on the abundance estimate we established, it is likely that moths migrating through the eastern front range of the GYE number in the billions. We conclude that the implementation of a moth monitoring program via radar should be considered, and we provide suggestions for future work.

Introduction

Migrating animals are important in the transport of energy, nutrients, and biomass between geographically distinct landscapes (Stepanian et al., 2020). Especially important among these are the insects, an often overlooked group (despite being the most species-rich animal on earth), perhaps owing partly to the difficulty in tracking their migration on account of their small size (Chapman et al., 2015). Migrating insects are of general interest because they are commonly agricultural pests (Chapman et al., 2015), or, conversely, charismatic species of conservation concern (Brower et al., 2012; May, 2013). Of the tools used in studying insect migration, radar has proved to be exceptionally insightful; resulting studies have upended some of our assumptions regarding insect migration and expanded our ability to monitor insect populations.

After its first successful use in tracking both orthopteran and lepidopteran migrants (Schaefer, 1969), radar has seen dramatic improvements. With the development of insect-specific radars such as the scanning insect radar and Vertical Looking Radar (VLR) came the ability to distinguish between individual organisms, and, consequently, determine the horizontal speed, displacement direction, body alignment, and approximate mass of insect targets (Chapman et al., 2003). Studies following this development were better able to characterize insect flight—rather than flying at the mercy of the wind (as was previously believed), it was illustrated that many insect migrants are sophisticated fliers. High-flying noctuids, such as *Autographa gamma* (L.), can assess wind direction and align their flight heading to both maximize their displacement speed and compensate for crosswind drift (Chapman et al., 2008a; Chapman et al., 2008b; Chapman et al., 2015). This was even found to be true of many large day- and night-flying insects (Chapman et al., 2010).

Radar has also facilitated the quantification of mass seasonal “bioflows” of insects, providing ecosystem-wide context for the exchange of nutrients between two disparate habitats (Hu et al., 2016). Furthermore, insect-specific monitoring is not limited exclusively to radars designed explicitly for insects. Given a detailed understanding of the life-history of an insect, a biomass estimate of an individual genus or species using radar intended for weather surveillance is also possible; an application of this approach was used to establish the first *Hexagenia* (burrowing mayflies) biomass estimates during their emergence period and monitor their flight between the Western Lake Erie Basin and Upper Mississippi River (Stepanian et al., 2020). Recent developments have even facilitated the discernment between birds and insects when using radars intended for weather surveillance (Nussbaumer et al., 2021), opening up decades of data gathered by the U.S. national network of WSR-88D Doppler radars for exploration of insect-specific questions.

Of the insect migrants for which there remain a multitude of questions regarding abundance and flight characteristics is the army cutworm moth, *Euxoa auxiliaris* (Lepidoptera: Noctuidae). This otherwise unassuming noctuid accomplishes the transport of billions of calories between two distinct biomes: the Great Plains of the United States and prairies of Canada, and the Rocky Mountains of the west (Pruess & Pruess, 1967). During their period spent in the plains, army cutworms are agricultural pests. In late September and early October, females return to the Great Plains of the United States and prairies of Canada to oviposit, and larvae emerge to begin feeding on a variety of both cultivated crops, weeds, and uncultivated plants (Burton et al., 1980; Cooley, 1916b; Pruess & Pruess, 1967; Strickland, 1916). After reaching their second instar, larvae overwinter by burrowing into the soil near host plants and emerge in the spring to continue feeding (Seamans, 1928b). Larvae pupate after reaching their seventh instar, and, after emerging as adults, begin their migration to the Rocky Mountains (Burton et al., 1980). This migration is thought to be triggered by the waning food sources and warming temperatures of their natal range (Pruess & Pruess, 1967).

Upon reaching the Rocky Mountains, army cutworm moths continue to feed on alpine blooms during the night, metabolizing the nectar into lipid stores reserved for the return flight to the plains and future oogenesis (Kevan & Kendall, 1997). Although some moths have been observed to feed during the day in the early summer (personal observation), most aggregate within the interstitial spaces of talus during the day to thermoregulate (French et al., 1994; White et al., 1998b). Aggregations of these ephemeral visitors constitute a significant portion of grizzly bear (*Ursus arctos horribilis*) diets, as this moth is one of the most calorically dense food resources within the Greater Yellowstone Ecosystem (GYE) (0.5 kcal/moth) (French et al., 1994; Gunther et al., 2014; White, 1999). Provided that moth density is sufficiently high, grizzly bears can consume as many as 40,000 moths per day (White, 1999), equating to roughly half of a bear's annual energy budget over the course of a 30 days (White, 1996).

Despite the importance of this moth in grizzly bear diets, moth abundance data collected in the moth's summering ranges are scarce. This paucity of abundance data is for good reason;

several researchers have attempted to characterize regional abundance at certain mountain peaks in the summering ranges of the moth using blacklight traps and/or hand excavation, but these efforts were so time- and effort-intensive that they were not continued beyond the scope of the study (French et al., 1994; O'Brien & Lindzey, 1994; Robison, 2009; White et al., 1998b). Researchers noted the difficulty of blacklight-trap maintenance in the high alpine, as the remote sites required hours of hiking each way. In some instances, access to moth aggregation sites was only feasible when backpacking.

Hand collection was complicated by the varied mobility of moths depending on ambient temperature of the talus, and it was often impossible to reach the bare soil that lay beneath the talus due to talus depth. Density counts also varied extensively due the heterogeneous nature of habitable moth sites (O’Brien & Lindzey, 1994; White et al., 1998b). This was only further complicated by the fluctuation of where moths aggregated in the talus; Robison (2009) noted that moths tracked changes in moisture throughout the summer season. Finally, because sampling efforts are typically conducted in areas of high moth density, grizzly bears were typically present at these sites. In addition to the risk posed to the research team by working in an area with a high density of bears, bears that encounter humans at these sites will typically cease foraging activities to run from the unknown threat—unnecessarily expending calories during a time that is critical for gaining fat (Nelson et al., 1983).

Thus, our understanding of abundance of army cutworm moths at aggregation sites is limited to general temporal abundance patterns (e.g., “high” vs. “low” abundance), several density counts conducted in different ranges during the 1990s, and abundance estimates from blacklight-trap collection. This lack of monitoring was first acknowledged in the Final

Conservation Strategy for the Grizzly Bear in the Greater Yellowstone Area (USFS, 2007), and executive mangers of the GYE have recognized that the current body of literature pertaining to army cutworm moth ecology is inadequate to manage grizzly bear foraging sites. In 2015, the USFS Land Management Plan for the Shoshone National Forest mandated that the ecology of the army cutworm moth be better explored through the collaboration of US Forest Service managers and other agencies. Subsequently, a project was developed to better address army cutworm moth ecology through the collaboration of staff from the USFS (SNF & the GYE Grizzly Bear Habitat Coordinator), staff from the USGS-Northern Rockies Science Center, and Montana State University (MSU).

Chief among the objectives of this project was the development of an army cutworm moth monitoring program at moth aggregation sites of interest. Consequently, our objectives for the development of this monitoring program included:

(1) Establish the viability of radar as a means to monitor army cutworm moth populations at moth aggregation sites.

(2) Estimate biomass of army cutworm moths using radar.

(3) Use radar to characterize flight patterns of army cutworm moths, including the general direction in which most moths were flying, the speed at which moths flew, and the nocturnal timeframe in which the highest amount of moth movement occurred.

(4) Gather circumstantial evidence that the nocturnal mass movements measured during 2020 and 2021 were army cutworm moths.

To complete these objectives, we monitored the airspace near a moth aggregation site of conservation interest with a modified marine radar in 2020 and 2021. Sampling was conducted during the time window preceding peak abundance of army cutworm moths at moth aggregation sites within the GYE. We established circumstantial evidence for army cutworm moth presence in the airspace during our sampling period by recording the frequency of army cutworm moth wingbeats in a laboratory setting and conducting a review of the existing literature.

Methods

Study area

Our study was conducted in the valley adjacent to a moth aggregation site that lies within the Absaroka Range of northwestern Wyoming (Figure 17). Because of disturbance concerns, we cannot identify this location (Nunlist, 2020b) and will instead refer to the mountain peak as "Peak A." Within the Absaroka Range, elevation ranges 1830-4006 m, wherein moth site elevations range 2700-3500 m (French et al., 1994; Mattson et al., 1991; White et al., 1998a). The geology of moth sites is dominated by talus fields that lack vegetation and lie beneath cliffs (French et al., 1994; Mattson et al., 1991; O'Brien & Lindzey, 1994). Moth populations are supported by neighboring patches of vegetation and meadows (French et al., 1994). Vegetation, climate, and geology have been described previously for this range (Baker, 1944; Dirks & Martner, 1982; Marston & Anderson, 1991; Sundell, 1993; Thilenius & Smith, 1985; Waddington & Wright, 1974).

Radar data collection

In 2020 and 2021, we sampled the airspace within 1 km of Peak A using a modified Furuno FAR2127BB marine radar (an X-band radar operating at 9.4 GHz with a wavelength of around 3 cm) that had been mounted into a pickup-truck bed (Figure 19). Upon arriving at our sampling location, we oriented the radar according to magnetic north (we adjusted for declination in post-processing). For a range of 3 km and 1500 m above the ground, images of the alpine airspace were taken by the radar every 2.5 seconds and logged by a computer (located within the truck cabin) for data analysis (Figure 17 & Figure 18).

The radar was run both day and night to contrast diurnal and nocturnal movements. Our 2020 sampling period began on 29 June 2020 and concluded the morning of 6 July 2020, and the 2021 sampling period began on 20 June 2021 and concluded on 5 July 2021. This timeframe was selected because it precedes peak moth abundance at moth aggregation sites within the GYE.

In 2020, the radar sampled with an antenna elevation of 40˚. After 1 July 2020, we switched the elevation of the radar antenna to 30˚ to better capture movement in the airspace. Sampling for the remainder of the 2020 period, excluding vertical sampling efforts conducted at night, was conducted at 30˚. In 2021, we set the antenna to an elevation of 30˚ during the entirety of the day and part of the night. For both 2020 and 2021, from 2200-0200 hours, we conducted "vertical sampling" by adjusting the elevation of the radar antenna to 90˚ (in which the radar was pointed directly upward and did not rotate). Vertical sampling was conducted during the nocturnal time frame in which we detected the largest amount of moth movement in 2020. This approach was used in an attempt to establish moth wingbeat rates.

In both 2020 and 2021, continuous sampling for the entirety of the sampling period was not possible due to intermittent lightning storms. The radar was turned off during these periods and restarted after the storms had cleared. In 2021, the radar only sampled during several hours or less of the day because data collected in 2020 illustrated that nocturnal and diurnal movements contrasted significantly. Post-processing of the images taken by the radar was conducted by R. Diehl and T. Preston.

Laboratory: Wingbeat measurements

Live army cutworm moths were hand-collected from Peak B (see Figure 4 of Chapter 2) on 7 July 2021 and placed into an aerated Tupperware container. Moths were transported to Bozeman at ambient temperatures, and 30 moths were held at ambient temperature in a 610 x 610 x 610 cm (24” x 24” x 24”) mosquito net cage until moths were prepared for wingbeat measurements. Moths were fed a sugar-water solution in the days leading up to measurements.

On 13 July 2021, 10 unsexed moths were randomly selected from the mosquito net cage and prepared for wingbeat frequency measurements. To prepare each moth, a pin was placed through the posterior end of the metathorax of the moth. This pin was held by a vice, and a piezoelectric microphone was held below the moth (Figure 20). After being secured by the pin and with the feet removed from a substrate, all moths “flew” readily. A sample of the ambient noise was taken before recording moth wingbeats; this sample was used to distinguish between the wingbeat frequency sampled from the moths and the background noise in which the measurements were taken. Moth wingbeat frequencies were measured for 20 s at a 10kHz sampling rate with 24 bits of precision. Data were recorded by a piezo-electric microphone and logged with a USB signal conditioner into MatLab. A Fast Fourier Transformation, considering a 10 s interval, was run on the voltage data.

Statistical analysis

All statistical analyses were conducted in R (Team, 2020). Directional data were handled with the circular package (Agostinelli & Lund, 2017).

Results

Radar

Only data collected from 2020 are reported here because data collected in 2021 have not yet undergone the post-processing step. For the 2020 sampling period, it was noted that there were extremely dense movements between 2200-0200 hours and within 160 – 750 m above ground level (AGL). Because target density was so high during this timeframe, the radar was sometimes unable to distinguish between individual samples. To circumvent this problem, we consulted R. Diehl to help create density estimates based on prior experience with data in this area. We generated a biomass estimate by assuming that moths were flying during five hours of the night (2200-0200 hours) and within 160-750 m AGL, producing an estimate of 2.1 million moths that were detected during that period. Nonetheless, this estimate was likely very conservative. After adjusting for the radar beam sampling area, it was estimated that about 5 million moths had passed through the sampling area (160-750 m AGL and 2600 m across), equating to approximately 70 moths per second.

Across all days of collection and during the period in which detected targets were likely primarily composed of moth migrants (2200-0200 hours), the mean direction of targets flying within 160-300 m AGL was southwest (260˚) (Table 7). This direction was consistent with moths flying toward the moth aggregation site (Peak A) located to the south of our sampling area. The mean direction of targets flying above this altitude and within this same time period was north to northwest, consistent with the direction of the other known moth aggregation site (Peak B). Similarly, the mean direction of targets flying within 750 m AGL during the day (1000-1400 hours) was most often northwest (Table 7). Above 750 m AGL, the mean direction of targets was primarily northeast. Some stratification was seen in the mean speed of detected targets during 2200-0200 hours (Table 8). Below 750 m AGL, targets tended to fly between 8 – 9 m/s; above 750 m AGL, targets flew faster with increasing altitude (up to 13 m/s).

Circumstantial evidence of army cutworm moths in the airspace

Primary indicators that army cutworm moths were the dominant organism in the airspace during the nocturnal period included the range of wingbeat frequencies that were measured at lower altitudes, differences in flight patterns between the nocturnal vs. diurnal sampling period, and the lack of other flying organisms during this timeframe, as indicated by the existing literature for this area (which we review below). The mean wingbeat frequency of army cutworm moth flight recorded in the laboratory setting was 41 Hz ± 4.27 ($n = 8$). These wingbeats were consistent with wingbeats that were measured at lower altitudes (< 750 m AGL); although wingbeat frequencies measured by radar were much more varied than anticipated, which suggest that some other organisms may be present. The strength of the radar echoes and vertical structure of the sampled organisms suggest that diurnal organisms were different from organisms sampled during the nocturnal period. Furthermore, the mean direction of organisms measured during the diurnal sampling period between 1000-1200 hours (302.3 ± 101.5) was different from the mean direction of organisms measured during the nocturnal sampling period during 2200-0200 hours (260.3 ± 94.0), only considering the targets within 160-300 m AGL.

A literature search pertaining to large migratory movements throughout the GYE yielded only studies detailing terrestrial movements (Middleton et al., 2020; Nelson et al., 2012; Nelson et al., 2016). Literature detailing migratory, night-flying insects within the Rocky Mountains mentioned only army cutworm moths (Chapman et al., 1955; French et al., 1994; Kevan &

Kendall, 1997; Mani, 1968; O'Brien & Lindzey, 1994). During the study, several species of moths that were likely endemic and non-migratory were hand-captured (personal observation), but it was unlikely that these moths were flying above the insect flight boundary layer, nor were they present in the same abundance as the army cutworm moth. The insect flight boundary layer is defined as the layer of atmosphere wherein an insect can fly in any direction, mostly unhampered by the wind (Chapman et al., 2011). Because most avian migration tends to occur throughout the fall or in the late winter and spring (Lincoln, 1935), we can likely conclude that army cutworm moths were the dominant organism during these periods of high flight activity, as our sampling period was conducted during part of their migratory window (June-July) (French et al., 1994; White, 1996).

Discussion

During both the 2020 and 2021 sampling period, the radar successfully monitored what were very likely army cutworm moths in the airspace. Considering only 20 hours of collection (which by no means encompasses the entirety of the migratory period of the moth), we estimate that 5 million moths passed through the 3-km wide plane of airspace sampled by the radar. In the context of the GYE, this represents only a fraction of the migration that is occurring. Using this estimate to consider just 100 km along the eastern front range of the GYE, and assuming that the amount of moth biomass passing through the airspace is similar for this entire range, the migratory period of the moth is a total of 25 movement nights (for which there are 5 hours of movement), and moths are moving within 160-750 m AGL, there are approximately 1.2 billion moths entering this relatively small alpine zone per summer. Using the estimate of White et al.

(1999) of 0.5 kcal/moth and 0.1 g/moth (dry weight), this would equate to around 600 million calories, weighing 120 metric tons.

In addition to providing an estimate of moth abundance, we were able to determine the mean direction and mean speed of the migrants. Within 160-300 m AGL and 2200-0200 hours, targets were moving roughly southwest toward Peak A, a known moth aggregation site. Above 300 m AGL, however, targets were moving northwest, potentially toward Peak B. Because there was so much variation seen in the direction of the detected targets during 2200-0200 (standard deviation was typically ~100˚), it is likely that (1) moths were flying in multiple directions, and (2) organisms in the airspace were not totally composed of moths, and thus were flying to a different location. These other organisms may have been bats. Moths tended to fly around 9 m/s as they approached the alpine area. Whether this speed is characteristic of the entirety of their migratory flight is unknown.

Several limitations are posed by the use of radar. Although we were able to estimate the number of migrants in the airspace, we do not yet understand how moths determine where they will land within these alpine aggregation sites. Assuming moths were flying directly toward a moth aggregation site might be incorrect, although it would seem most efficient for moths to land as soon as they have reached a mountainous area that is habitable. With permission of the managers of the Shoshone National Forest, future efforts could include hand-collection within the talus in concert with the radar monitoring effort to establish the relationship between the abundance estimated by the radar and the subsequent amount of food made available to grizzly bears at these sites.

Further refinements, such as altering the sampling plane to include targets moving within the lower 160 m of airspace, using lidar to resolve the accuracy of the radar’s estimates, and using three (rather than one) radars stationed along the eastern front range of the GYE, would also help improve the accuracy of reported measurements. Given the success of this effort, data generated by the U.S. national network of WSR-88 Doppler radars should also be explored for noctuid-like movements during the migratory period of the army cutworm moth; this information could help improve our understanding of both historical and current abundance for a much broader range. Finally, and most critically, the confirmation that the detected targets are indeed army cutworm moths should be established with direct aerial sampling.

Previously, estimating army cutworm moth abundance was restricted to time-intensive, and potentially hazardous, hand-sampling or blacklight sampling efforts conducted in the high alpine. Although these efforts provided a better understanding of the variation of intra-site moth abundance, comparability between years was limited due to the heterogeneity of these sites. Here, we presented evidence for an alternative method for estimating army cutworm moth abundance that is non-invasive and capable of providing more comprehensive abundance estimates. Beyond establishing a monitoring program for moth abundance at moth aggregation sites, and thus fulfilling the directive of the USFS Land Management Plan for the Shoshone National Forest (2015), future monitoring efforts can also be used to address some of our remaining questions about moth migration.

Table 7: The mean direction of migrants detected by the radar unit located 1 km outside of Peak A per: (1) the altitudinal stratum at which the targets were flying and (2) the time frame (either 2200 – 0200 hours and 1000 – 1400 hours) during which the targets were flying. Data were collected from 29 June 2020-6 July 2020.

	2300 – 0200 hours	1000 – 1400 hours
Altitude (m)	Mean ± SD (degrees)	Mean ± SD (degrees)
160-300	260.3 ± 94.0	302.3 ± 101.5
300-450	303 ± 108.4	302.4 ± 102.6
450-600	333.3 ± 118.2	304.6 ± 102.9
600-750	3.0 ± 129.9	308.2 ± 107.6
750-900	1.76 ± 129.3	344.8 ± 113.6
900-1050	336 ± 120.6	51.8 ± 109.6
1050-1200	329.6 ± 114.8	66.7 ± 96.6
1200-1350	331.5 ± 114.0	71.1 ± 83.8
1350-1500	336.3 ± 116.8	69.7 ± 81.9

Table 8: The mean speed (m/s) of migrants detected by the radar unit located 1 km outside of Peak A during 29 June-6 July 2020 and between the hours 2200-0200. Mean speed of the targets was calculated for the average of each altitudinal stratum.

Altitude (m)	Mean ± SD (m/s)
160-300	9.4 ± 4.6
300-450	9.2 ± 4.7
450-600	8.5 ± 4.5
600-750	9.3 ± 4.5
750-900	9.8 ± 4.4
900-1050	10.9 ± 4.5
1050-1200	12.0 ± 4.5
1200-1350	12.6 ± 4.2
1350-1500	13.0 ± 4.0

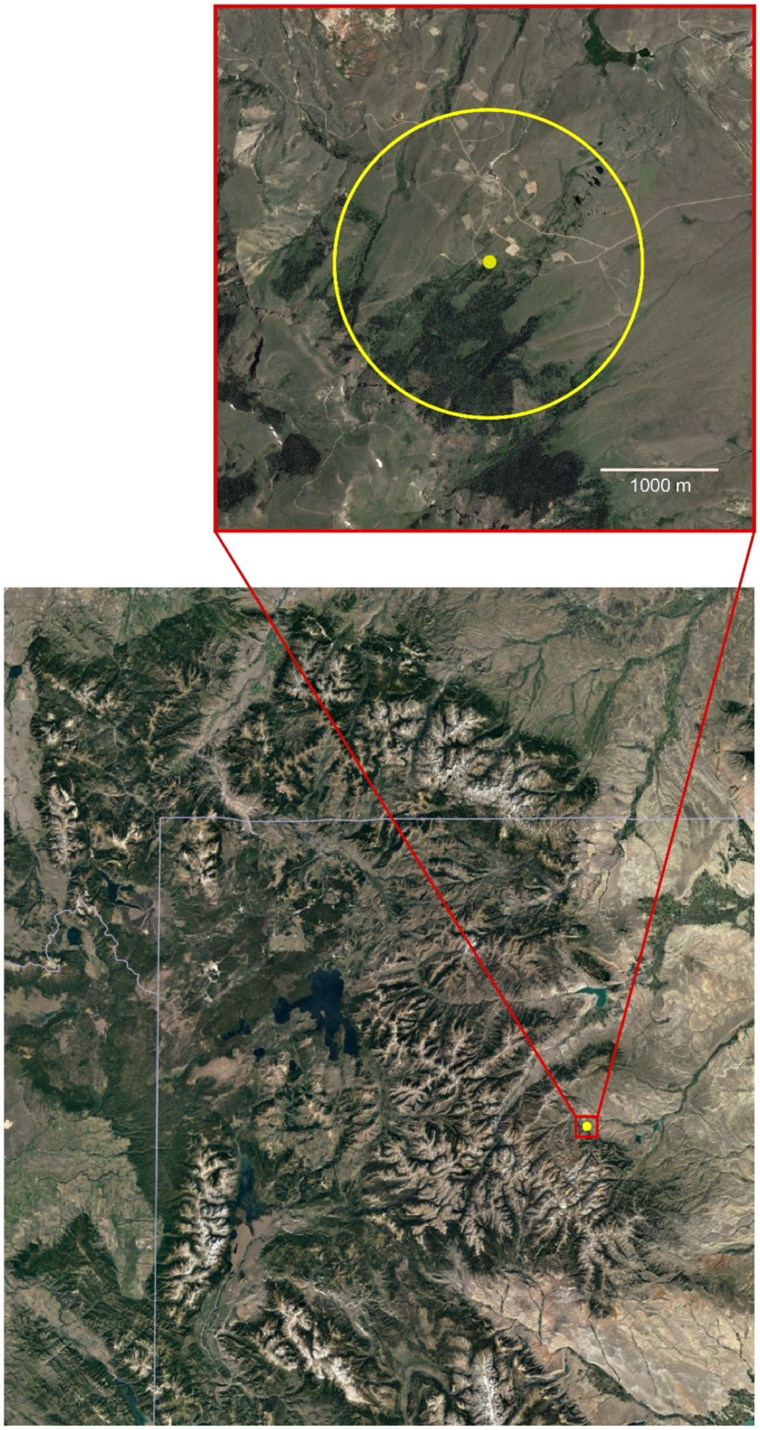
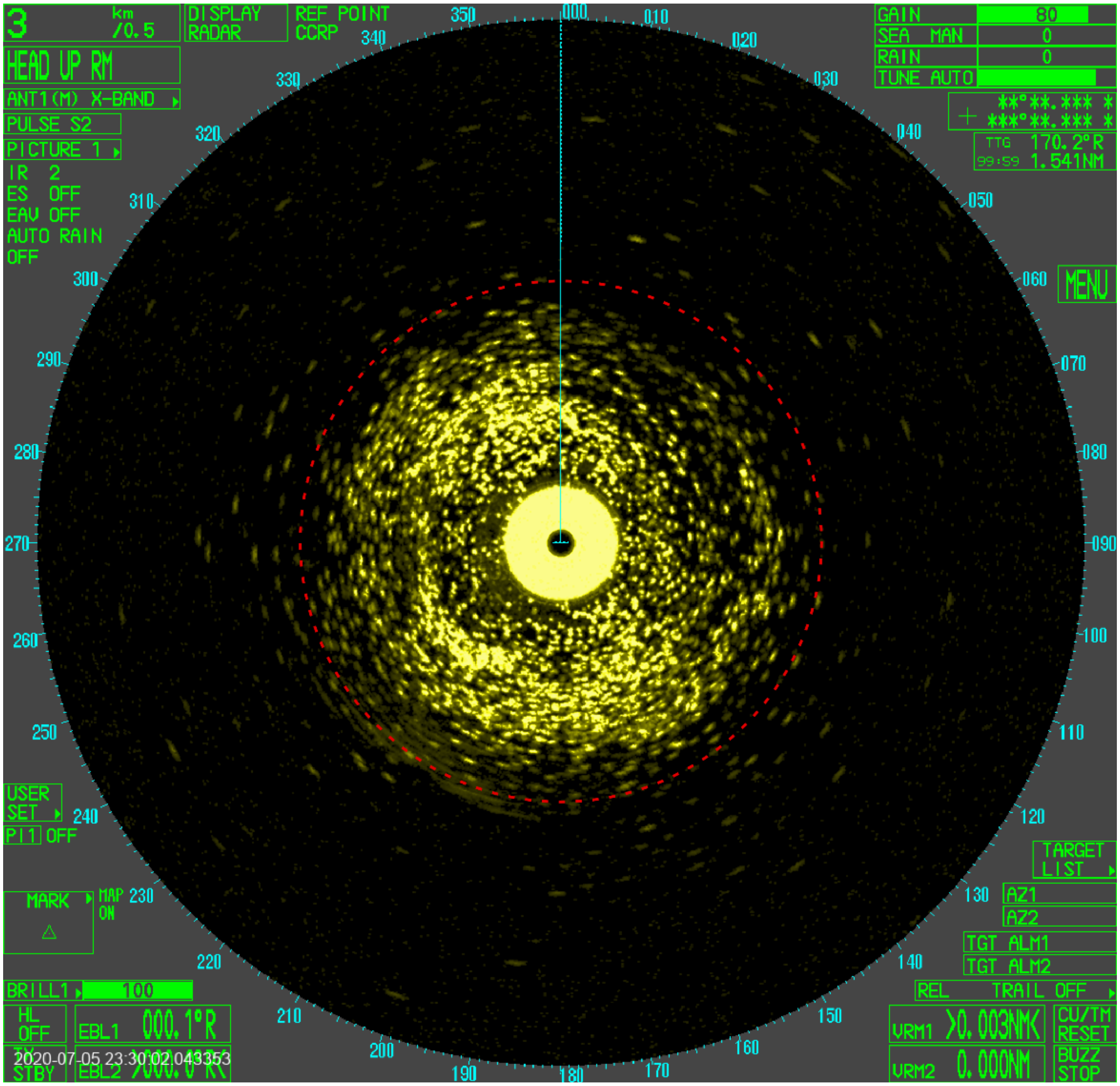


Figure 17: Portable radar coverage in the Shoshone National Forest (above), and its position within the Greater Yellowstone Ecosystem (below). The yellow dot illustrates the coverage area. From Dr. Robert H. Diehl.



3 km /0.5
DISPLAY RADAR
REF POINT CCRP
HEAD UP RM
ANT1(M) X-BAND
PULSE S2
PICTURE 1
IR 2
ES OFF
EAV OFF
AUTO RAIN OFF
GAIN 80
SEA MAN 0
RAIN 0
TUNE AUTO
°.*** *
°**. *
TTG 99:59 170.2°R 1.541NM
USER SET
PI1 OFF
MAP ON
BRILL1 100
HL OFF
TX STBY
EBL1 000.1°R
EBL2 >000.0°R<
REL TRAIL OFF
VRM1 >0.003NM<
VRM2 0.000NM
2020-07-05 23:30:02.043353

Figure 18: An image taken by the radar. The radar is located in the middle of the circular coverage area, and targets are recorded as individual yellow dots. The maximum range from the radar to the periphery of the coverage area is 3 km. The dashed red line indicates 1.5 km range from the radar, corresponding to a height of 750 m above the ground.

Figure 19: An image of the transportable radar unit at our study site.

Figure 20: Setup for the wingbeat frequency measurements using a piezoelectric microphone. An army cutworm moth, suspended on a pin, was held by a vice (upper left). A piezoelectric microphone was placed underneath the moth to measure wingbeat frequency.

REFERENCES CITED

Agostinelli, C., & Lund, U. (2017). R package 'circular': Circulat statistics (version 0.4-93). https://r-forge.r-project.org/projects/circular/

Arritt, R. W., Rink, T. D., Segal, M., Todey, D. P., Clark, C. A., Mitchell, M. J., & Labas, K. M. (1997). The Great Plains low-level jet during the warm season of 1993. *Monthly Weather Review, 125*, 2176-2192.

Augustine, D., Davidson, A., Dickinson, K., & Van Pelt, B. (2021). Thinking like a grassland: Challenges and opportunities for biodiversity conservation in the Great Plains of North America. *Rangeland Ecology & Management, 78*, 281-295.

Baker, F. S. (1944). Mountain climates of the western United States. *Ecological Monographs, 14*(2), 223-254.

Basara, J. B., Maybourn, J. N., Peirano, C. M., Tate, J. E., Brown, P. J., Hoey, J. D., & Smith, B. R. (2013). Drought and associated impacts in the Great Plains of the United States—A review.

Beerwinkle, K. R., Lopez, J. D., JR., Witz, J. A., Schleider, P. G., Eyster, R. S., & Lingren, P. D. (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, B. P. (1970). Effects of precipitation on crop insects. *The Canadian Entomologist, 102*(11), 1360-1373.

Blodgett, S. (1997). *Pheromone traps help forecast cutworm moth activity* (Montana Crop Health Report, Issue.

Blodgett, S., Lanier, W. T., & Johnson, G. D. (2003). *IPM Western Region Cutworm Survey and Risk Warning 2003 Report*. Montana State University. http://scarab.msu.montana.edu/Cutworm/CW2003.htm

Bowen, G. J., Ehleringer, J. R., Chesson, L. A., Stange, E., & Cerling, T. E. (2007). Stable isotope ratios of tap water in the contiguous United States. *Water Resources Research, 43*(3).

Bowen, G. J., Wassenaar, L. I., & Hobson, K. A. (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia, 143*(3), 337-348.

Brattström, O., Bensch, S., Wassenaar, L. I., Hobson, K. A., & Åkesson, S. (2010). Understanding the migration ecology of European red admirals Vanessa atalanta using stable hydrogen isotopes. *Ecography, 33*(4), 720-729.

Brower, L. P., Taylor, O. R., Williams, E. H., Slayback, D. A., Zubieta, R. R., & Ramirez, M. I. (2012). Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity, 5*(2), 95-100.

Burton, R. L., Starks, K., & Peters, D. (1980). The Army Cutworm. *Oklahoma Agricultural Experiment Station*(Bulletin No. B749).

Carter, P. R., Hicks, D. R., Oplinger, E. S., Doll, J. D., Bundy, L. G., Schuler, R. T., & Holmes, B. J. (1989). Grain Sorghum (Milo). *Alternative Field Crops Manual*.

Chapman, J. A., Romer, J. I., & Stark, J. (1955). Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology, 36*(1), 156-158.

Chapman, J. W., Drake, V. A., & Reynolds, D. R. (2011). Recent insights from radar studies of insect flight. *Annual Review of Entomology, 56*, 337-356.

Chapman, J. W., Nesbit, R. L., Burgin, L. E., Reynolds, D. R., Smith, A. D., Middleton, D. R., & Hill, J. K. (2010). Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science, 327*(5966), 682-685.

Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008a). A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology, 18*(19), R908-R909.

Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008b). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology, 18*(7), 514-518.

Chapman, J. W., Reynolds, D. R., & Smith, A. D. (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, J. W., Reynolds, D. R., & Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecology letters, 18*(3), 287-302.

Choate, C. M. (1963). *Ordination of the Alpine plant communities at Logan Pass Glacier National Park Montana* Montana State University].

Common, I. (1954). A study of the ecology of the adult bogong moth, Agrotis infusa (Boisd)(Lepidoptera: Noctuidae), with special reference to its behaviour during migration and aestivation. *Australian journal of zoology, 2*(2), 223-263.

Cook, W. C. (1927). Studies in the ecology of Montana cutworms (Phalaenidae). *Ecology, 8*, 158-173.

Cooley, R. A. (1910). *The army cutworm* (Vol. 4). Montana Agricultural College, Experiment Station.

Cooley, R. A. (1916a). Observations on the life history of the army cutworm, Chorizagrotis auxiliaris. *J. Agric. Res, 6*, 871-881.

Cooley, R. A. (1916b). Observations on the life history of the army cutworm, Chorizagrotis auxiliaris. *Journal of Agricultural Resources, 6*, 871-881.

Coop, J. D., Hibner, C. D., Miller, A. J., & Clark, G. H. (2005). Black bears forage on army cutworm moth aggregations in the Jemez Mountains, New Mexico. *The Southwestern Naturalist, 50*(2), 278-281.

Crum, T. D., & Alberty, R. L. (1993). The WSR-88D and the WSR-88D operational support facility. *Bulletin of the American Meteorological Society, 74*(9), 1669-1688.

Damm, C. (2001). *A Phytosociological Study of Glacier National Park, Montana, U.S.A., with Notes on the Syntaxonomy of Alpine Vegetation in Western North America* Georg-August-Universität zu Göttingen].

Dirks, R. A., & Martner, B. E. (1982). *The climate of Yellowstone and Grand Teton National Parks*. US Department of the Interior, National Park Service.

Endler, J. A. (1973). Gene flow and population differentiation. *Science, 179*, 243-250.

Finklin, A. I. (1986). *A Climatic Handbook for Glacier National Park: With Data for Waterton Lakes National Park* (Vol. 204). US Department of Agriculture, Forest Service, Intermountain Research Station.

Flockhart, D. T., Brower, L. P., Ramirez, M. I., Hobson, K. A., Wassenaar, L. I., Altizer, S., & Norris, D. R. (2017). Regional climate on the breeding grounds predicts variation in the natal origin of monarch butterflies overwintering in Mexico over 38 years. *Global change biology, 23*(7), 2565-2576.

Flockhart, D. T., Wassenaar, L. I., Martin, T. G., Hobson, K. A., Wunder, M. B., & Norris, D. R. (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceedings of the Royal Society B: Biological Sciences, 280*(1768), 20131087.

Fortin, J. K., Schwartz, C. C., Gunther, K. A., Teisberg, J. E., Haroldson, M. A., Evans, M. A., & Robbins, C. T. (2013). Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of Wildlife Management, 77*(2), 270-281.

French, S. P., French, M. G., & Knight, R. R. (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, C. P. (1903). *Some of the more important insects of 1903* (Vol. 94). Bulletin of the Colorado Agriculture Experiment Station

Gunther, K. A., Shoemaker, R. R., Frey, K. L., Haroldson, M. A., Cain, S. L., Van Manen, F. T., & Fortin, J. K. (2014). Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus*, 61-73.

Hardwick, D., & Lefkovitch, L. (1971). Physical and biotic factors affecting Euxoa species abundance in western North America: a regression analysis. *The Canadian Entomologist, 103*(9), 1217-1235.

Heinrich, K., & Collins, L. (2017). Determining the geographical origin of Asian longhorn beetle (Anoplophora glabripennis) specimens using stable isotope and trace element analyses. *Pest management science, 73*(5), 967-975.

Hendrix III, W., Mueller, T., Phillips, J., & Davis, O. (1987). Pollen as an indicator of long-distance movement of Heliothis zea (Lepidoptera: Noctuidae). *Environmental entomology, 16*(5), 1148-1151.

Hobson, K., Wassenaar, L. I., Mila, B., Lovette, I., Dingle, C., & Smith, T. B. (2003). Stable isotope as indicators of altitudinal distributions and moevments in an Ecuadorean hummingbird community. *Oecologia, 136*, 302-308.

Hobson, K. A., Doward, K., Kardynal, K. J., & McNeil, J. N. (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.

Hobson, K. A., Kusack, J. W., Gootgarts, J., Longstaffe, F. J., & McNeil, J. N. (2022). Using stable isotopes (δ 2H, δ 13C) to identify natal origins and larval host plant use by western bean cutworm, Striacosta albicosta (Lepidoptera: Noctuidae) captured in southern Ontario. *Ecological Entomology*.

Hobson, K. A., & Norris, D. R. (2008). *Animal migration: a context for using new techniques and approaches. Tracking animal migration with stable isotopes*. Academic Press.

Hobson, K. A., Soto, D. X., Paulson, D. R., Wassenaar, L. I., & Matthews, J. H. (2012). A dragonfly (δ2H) isoscape for North America: a new tool for determining natal origins of migratory aquatic emergent insects. *Methods in ecology and evolution, 3*(4), 766-772.

Hobson, K. A., & Wassenaar, L. I. (2019). *Tracking animal migration with stable isotopes*. Academic Press.

Hobson, K. A., Wassenaar, L. I., & Taylor, O. R. (1999, 1999/08/01). Stable isotopes (δD and δ13C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia, 120*(3), 397-404. https://doi.org/10.1007/s004420050872

Holder, P. W., Armstrong, K., Van Hale, R., Millet, M.-A., Frew, R., Clough, T. J., & Baker, J. A. (2014). Isotopes and trace elements as natal origin markers of Helicoverpa armigera–an experimental model for biosecurity pests. *PloS one, 9*(3), e92384.

Hu, G., Lim, K. S., Horvitz, N., Clark, S. J., Reynolds, D. R., Sapir, N., & Chapman, J. W. (2016). Mass seasonal bioflows of high-flying insect migrants. *Science, 354*(6319), 1584-1587.

Hyodo, F. (2015). Use of stable carbon and nitrogen isotopes in insect trophic ecology. *Entomological Science, 18*(3), 295-312.

IGBST. (2020). Yellowstone Grizzly Bear Investigations

Jacobson, L. A., & Blakeley, P. E. (1959). Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America, 52*(1), 100-105.

Johnson, S. A. (1905). Cutworms. *Colorado Experiment Station Bulletin, No. 98.*

Kendall, D. M. (1981). *Bionomics of Euxoa auxiliaris Grote (Lepidoptera: Noctuidae) in the Rocky Mountains and comparison with two resident species of alpine moths* University of Colorado (at Colo. Spgs.].

Kendall, D. M., Kevan, P. G., & LaFontaine, J. D. (1981). Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist, 113*(7), 607-614.

Kevan, P. G., & Kendall, D. M. (1997, 1997/11/01). 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://doi.org/10.1080/00040851.1997.12003268

Koel, T. M., Bigelow, P. E., Doepke, P. D., Ertel, B. D., & Mahony, D. L. (2005). Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries, 30*(11), 10-19.

Koerwitz, F., & Pruess, K. (1964). Migratory potential of the army cutworm. *Journal of the Kansas Entomological Society, 37*(3), 234-239.

Kucharik, C. J. (2006). A multidecadal trend of earlier corn planting in the central USA. *Agronomy Journal, 98*(6), 1544-1550.

Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., Kruk, M. C., Thomas, D., Shulski, M., & Umphlett, N. A. (2013). Regional climate trends and scenarios for the US National Climate Assessment Part 4. Climate of the US Great Plains.

Lafontaine, J. (1987). *The Moths of North America North of Mexico. Fascicle 27.2. Noctuoidea Noctuidae (Part)*. The Wedge Entomological Foundation Washington.

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., & Yeager, L. A. (2012). Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological reviews, 87*(3), 545-562.

Lincoln, F. C. (1935). *The migration of North American birds*. US Department of Agriculture.

Ma, C., Vander Zanden, H. B., Wunder, M. B., & Bowen, G. J. (2020). assignR: An r package for isotope-based geographic assignment. *Methods in ecology and evolution, 11*(8), 996-1001.

Manen, F. T. v., Haroldson, M. A., Bjornlie, D. D., Erbinger, M. R., Thompson, D. J., Costello, C. M., & White, G. C. (2016). Density Dependence, Whitebark Pine, and Vital Rates of Grizzly Bears. *The Journal of Wildlife Management, 80*(2), 300-313.

Mani, M. S. (1962). *Introduction to High Altitude Entomology*. Methuen & Co.

Mani, M. S. (1968). *Ecology and biogeography of high altitude insects* (Vol. 4). Springer Science & Business Media.

Marshall, J. D., Brooks, J. R., & Lajtha, K. (2007). *Sources of variation in the stable isotopic composition of plants*. Blackwell.

Marston, R. A., & Anderson, J. E. (1991). Watersheds and vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology, 5*(3), 338-346.

Mattson, D. J., Gillin, C. M., Benson, S. A., & Knight, R. R. (1991). Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology, 69*(9), 2430-2435.

May, M. L. (2013). A critical overview of progress in studies of migration of dragonflies (Odonata: Anisoptera), with emphasis on North America. *Journal of Insect Conservation, 17*(1), 1-15.

McNabb, D. M., Halaj, J., & Wise, D. H. (2001). Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. *Pedobiologia, 45*(4), 289-297.

Middleton, A. D., Sawyer, H., Merkle, J. A., Kauffman, M. J., Cole, E. K., Dewey, S. R., Gude, J. A., Gustine, D. D., McWhirter, D. E., & Proffitt, K. M. (2020). Conserving transboundary wildlife migrations: recent insights from the Greater Yellowstone Ecosystem. *Frontiers in Ecology and the Environment, 18*(2), 83-91.

Morrill, W. (1991). Montana small grain insects: armyworms and cutworms. *Montana Agriculture Experiment Station, Montana State University, Bozeman, Capsule Information Ser*(34).

Nelson, A. A., Kauffman, M. J., Middleton, A. D., Jimenez, M. D., McWhirter, D. E., Barber, J., & Gerow, K. (2012). Elk migration patterns and human activity influence wolf habitat use in the Greater Yellowstone Ecosystem. *Ecological Applications, 22*(8), 2293-2307.

Nelson, A. A., Kauffman, M. J., Middleton, A. D., Jimenez, M. D., McWhirter, D. E., & Gerow, K. (2016). Native prey distribution and migration mediates wolf (Canis lupus) predation on domestic livestock in the Greater Yellowstone Ecosystem. *Canadian Journal of Zoology, 94*(4), 291-299.

Nelson, R. A., Folk Jr, G. E., Pfeiffer, E. W., Craighead, J. J., Jonkel, C. J., & Steiger, D. L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management*, 284-290.

Nunlist, E. (2020a). *Grizzly Bears and Humans at Two Moth Aggregation Sites in Wyoming* Montana State University]. Bozeman, Montana.

Nunlist, E. (2020b). *Grizzly Bears and Humans at Two Moth Aggregation Sites in Wyoming.* Montana State University].

Nussbaumer, R., Schmid, B., Bauer, S., & Liechti, F. (2021). A Gaussian mixture model to separate birds and insects in single-polarization weather radar data. *Remote Sensing, 13*(10), 1989.

O'Brien, S. L., & 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.

O'Brien, S. L., & Lindzey, F. G. (1998). Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*, 427-435.

Oku, T., Chiba, T., & Fuse, H. (1983). Phenology and behaviour of cutworms, *Euxoa sibirica* Boisduval and *E. oberthueri* Butler (Lepidoptera, Noctuidae), in Tohoku district: II. Seasonal trap catches of adults in relation to aestival diapause and migration. *Kontyû, 51*, 144-157.

Oku, T., Saito, O., Fuse, H., & Chiba, T. (1982). Phenology and behavior of cutowrms, *Euxoa sibirica* Boisduval and *E. oberthueri* Buter (Lepidoptera, Noctuidae), in Tohoku district: I. Seasonal trap cataches of adults in relation to aestival diapause and migration. *Kontyû, 50*, 301-313.

Omernik, J. M., & Griffith, G. E. (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environmental management, 54*(6), 1249-1266.

Pardo, L. H., & Nadelhoffer, K. J. (2010). Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. In *Isoscapes* (pp. 221-249). Springer.

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.

Pogue, M. G., & Simmons, R. B. (2008). A new pest species of Copitarsia (Lepidoptera: Noctuidae) from the neotropical region feeding on Asparagus and cut flowers. *Annals of the Entomological Society of America, 101*(4), 743-762.

Ponsard, S., Bethenod, M.-T., Bontemps, A., Pélozuelo, L., Souqual, M.-C., & Bourguet, D. (2004). Carbon stable isotopes: a tool for studying the mating, oviposition, and spatial distribution of races of European corn borer, Ostrinia nubilalis, among host plants in the field. *Canadian Journal of Zoology, 82*(7), 1177-1185.

Prasifka, J., & Heinz, K. (2004). The use of C3 and C4 plants to study natural enemy movement and ecology, and its application to pest management. *International Journal of Pest Management, 50*(3), 177-181.

Pruess, K., & Pruess, N. C. (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.

Pruess, K. P., & Pruess, N. C. (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.

Quinby, B. M., Creighton, J. C., & Flaherty, E. A. (2020). Stable isotope ecology in insects: a review. *Ecological Entomology, 45*(6), 1231-1246.

Reynolds, D., & Riley, J. (1997). *Flight behaviour and migration of insect pests. Radar studies in developing countries*. Natural Resources Institute (NRI).

Robinson, E. B., & Dietz, J. L. (2020). *Great Plains*. https://www.britannica.com/place/Great-Plains

Robison, H. L. (2009). *Relationships between Army Cutworm Moths and Grizzly Bear Conservation* University of Nevada, Reno].

Robison, H. L., Schwartz, C. C., Petty, J. D., & Brussard, P. F. (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.

Rosenberg, N. J. (1987). Climate of the Great Plains region of the United States. *Great Plains Quarterly*, 22-32.

Schaefer, G. (1969). Radar studies of locust, moth and butterfly migration in the Sahara. *Proc Royal Entomol Soc Lond C, 34*(33), 39-40.

Schwartz, C. C., Fortin, J. K., Teisberg, J. E., Haroldson, M. A., Servheen, C., Robbins, C. T., & Van Manen, F. T. (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.

Seamans, H. (1928a). Forecasting Outbreaks of the Army Cutworm (Chonzagrotis auxiliaris, Grote). *Forecasting Outbreaks of the Army Cutworm (Chonzagrotis auxiliaris, Grote).*

Seamans, H. (1928b). Forecasting Outbreaks of the Army Cutworm (Chorizagrotis auxiliaris, Grote). *Annual Report of the Entomological Society of Ontario, 58*, 76-85.

Shapiro, A., & Fedorovich, E. (2008). Coriolis effects in homogeneous and inhomogeneous katabatic flows. *Quarterly Journal of the Royal Meteorological Society, 134*.

Shapiro, A., Fedorovich, E., & Rahimi, S. (2016). A Unified Theory for the Great Plains Nocturnal Low-Level Jet. *Journal of Atmospheric Sciences, 73*, 3037-3057.

Showers, W. B., Smelser, R. B., Keaster, A. J., Whitford, F., Robinson, J. F., Lopez, J. D., & Taylor, S. E. (1989a). Recapture of marked black cutworm (Lepidoptera: Noctuidae) males after long-range transport. *Environmental entomology, 18*(3), 447-458.

Showers, W. B., Whitford, F., Smelser, R. B., Keaster, A. J., Robinson, J. F., Lopez, J. D., & Taylor, E. S. (1989). Direct Evidence for Meteorologially Driven Long-Range Dispersal of an Economically Important Moth. *Ecology, 70*, 987-992.

Snow, S. J. (1925). Observations on the cutworm, *Euxoa auxiliaris* Grote, and its principal parasites. *Journal of Economic Entomology, 18*(4), 602-609.

Song, J., Liao, K., Coulter, R. L., & Lesht, B. M. (2005). Climatology of the low-level jet at the Southern Great Plains Atmospheric Boundary Layer Experiments site. *Journal of Applied Meteorology 44*, 1593-1606.

Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016). Long-distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology letters, 12*(10), 20160561.

Stepanian, P. M., Entrekin, S. A., Wainwright, C. E., Mirkovic, D., Tank, J. L., & Kelly, J. F. (2020). Declines in an abundant aquatic insect, the burrowing mayfly, across major North American waterways. *Proceedings of the National Academy of Sciences, 117*(6), 2987-2992.

Strickland, E. H. (1916). *The Army Cutworm: Euxoa (Chorizagrotis) Auxiliaris Grote* (Vol. Bulletin 13). Canadian Department of Agricultural Entomology.

Sundell, K. A. (1993). *Geology of Wyoming: Geological Survey of Wyoming Memoir No. 5*.

Team, R. C. (2020). *R: A language and environment for statistical computing.* In R Foundation for Statistical Computing. https://www.R-project.org/

Terzer, S., Wassenaar, L. I., Araguás-Araguás, L. J., & Aggarwal, P. K. (2013). Global isoscapes for δ18O and δ2H in precipitation: improved prediction using regionalized climatic regression models. *Hydrology and Earth System Sciences, 17*(11), 4713-4728. https://doi.org/10.5194/hess-17-4713-2013

Thilenius, J. F., & Smith, D. R. (1985). Vegetation and soils of an alpine range in the Absaroka Mountains, Wyoming. *US Dept of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station*, 1-23.

Triplehorn, C. A., Johnson, N. F., & Borror, D. J. (2005). *Borror and DeLong's Introduction to the Study of Insects*.

University of Nebraska, L. (2020). *Light Trap Data*. https://entomology.unl.edu/fldcrops/lightrap

USDA. (1951-1975). Cooperative Economic Insect Report.

USDA. (2022). *United States — Crop Production Maps*. https://ipad.fas.usda.gov/rssiws/al/us_cropprod.aspx

USFS. (2007). Final conservation strategy for the grizzly bear in the Greater Yellowstone Area.

USFS. (2015). Land Management Plan 2015 Revision.

Waddington, J. C., & Wright, H. (1974). Late Quaternary Vegetational Changes on the East Side of Yellowstone Park, Wyoming1. *Quaternary Research, 4*(2), 175-184.

Walkden, H. H. (1942). *Owlet moths (Phalaenidae) taken at light traps in Kansas and Nebraska*. US Department of Agriculture.

Walkden, H. H. (1950). *Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains*.

Walters, C. K., Winkler, J. A., Shadbolt, R. P., Ravensway, J. v., & Bierly, G. D. (2008). A long-term climatology of southerly and northerly low-level jets for the central United States. *Annals of the American Association of Geographers, 98*, 521-552.

Warrant, E., Frost, B., Green, K., Mouritsen, H., Dreyer, D., Adden, A., Brauburger, K., & Heinze, S. (2016). The Australian Bogong moth Agrotis infusa: a long-distance nocturnal navigator. *Frontiers in Behavioral Neuroscience, 10*, 77.

Wassenaar, L. (2009). *Manual for the Use of Stable Isotopes in Entomology*. International Atomic Energy Agency.

Wassenaar, L. I., & Hobson, K. A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences, 95*(26), 15436-15439.

Wassenaar, L. I., & Hobson, K. A. (2000). Improved method for determining the stable-hydrogen isotopic composition (dD) of complex organic materials of environmental interest. *Environmental Science and Technology, 34*, 2354-2360.

Wassenaar, L. I., & Hobson, K. A. (2003). Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopic in Environmental and Health Studies, 39*.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution, 17*(2), 76-83.

West, J. B., Bowen, G. J., Cerling, T. E., & Ehleringer, J. R. (2006). Stable isotopes as one of nature's ecological recorders. *Trends in Ecology & Evolution, 21*(7), 408-414.

West, J. B., Bowen, G. J., Dawson, T. E., & Tu, K. P. (2009). *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer.

Westbrook, J., & Wolf, W. (1998). Migratory flights of bollworms, Helicoverpa zea (Boddie), indicated by Doppler weather radar. Preprints-Weather Data Requirements for Integrated Pest Management: 23rd Conference on Agricultural and Forest Meteorology, 2nd Urban Environment Symposium, and 13th Conference on Biometeorology and Aerobiology,

Westbrook, J. K. (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, D. D. (1996). *Two grizzly bear studies: moth feeding ecology and male reproductive biology* [PhD, Montana State University-Bozeman, College of Letters & Science].

White, D. D. K., K.C..; and Picton, H.D. (1999). Potential Energetic Effects of Mountain Climbers on Foraging Grizzly Bears. *Wildlife Society Bulletin (1973-2006), 27*, 146-151.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998a). Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology, 76*(2), 221-227.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998b). Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology, 76*(5), 835-842.

Willis, B. (1902). Stratigraphy and structure, Lewis and Livingston ranges, Montana. *Bulletin of the Geological Society of America, 13*(1), 305-352.

Wood, C. R., Chapman, J. W., Reynolds, D. R., Barlow, J. F., Smith, A. D., & Woiwod, I. P. (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.

Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In *Isoscapes* (pp. 251-270). Springer.

Yang, L. H., Ostrovsky, D., Rogers, M. C., & Welker, J. M. (2016). Intra-population variation in the natal origins and wing morphology of overwintering western monarch butterflies Danaus plexippus. *Ecography, 39*(10), 998-1007.

CHAPTER FOUR

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Summary

The purpose of this project was to obtain information necessary for management decisions pertaining to moth aggregation sites in the GYE. Here, we summarize our major findings and management recommendations.

Natal origin and larval feeding habits (Absaroka Range)

Our primary objective was to determine whether army cutworm moths collected in the Absaroka Range were migrating exclusively from a subpopulation within the Great Plains using stable hydrogen. This was to assess whether moth populations at moth aggregation sites are potentially imperiled by periodic declines in subpopulations that "supply" their respective moth aggregation sites. Our other objectives were to characterize the natal origins of moths collected from two mountain ranges, the Absaroka Range and the Lewis Range, establish the migratory patterns of moths as they fly to the Rocky Mountains from the Great Plains, and characterize the larval feeding habits of moths collected in the Absaroka Range. Because this summary serves to provide management suggestions for managers of the Greater Yellowstone Ecosystem, we have chosen to exclude findings regarding the Lewis Range.

The probable natal origins of army cutworm moths collected from mountain peaks within the GYE were far more varied than we anticipated. Rather than moving exclusively east-west, there was strong evidence that army cutworm moths were also migrating north-south. Of the mountain peaks that we sampled in the Absaroka Range, most migrants had the highest probability of origin in Canada, including Alberta, Saskatchewan, British Columbia, part of Manitoba, and the very southern border of the Northwest Territories for all years. In the United States, probability of origin was also found to be moderate to high within Montana, Wyoming, and Idaho for all years. However, army cutworm moths may have originated from the entirety of their potential range throughout the Great Plains in years that were characterized with highly variable probable origins (i.e., varied δ^2H wing values). Because some years were composed of such light δ^2H wing values, there was limited comparability with the predictive mean δ^2H wing map; assignments generated for samples with wing values less than -150‰ may not be accurate. Nonetheless, given the large variation we saw in mean δ^2H wing values throughout the years in which we collected, there is very strong evidence that moth populations were supplied by multiple locations. Thus, moth populations at moth aggregation sites are likely insulated against regional declines that may occur in specific populations within the Great Plains.

During their larval period in the Great Plains, it was noted that almost all moths collected in the Absaroka Range fed exclusively on C3 plants, as indicated by their δ^{13}C values. Thus, we can conclude that few moths feed upon C4 prairie grasses or corn during their larval stages, despite their generalist feeding habits that were noted in much of the literature. Although stable nitrogen results were not as clear, it was also evident that very few moths fed in heavily fertilized agroecosystems. These findings likely suggest that larval army cutworm populations are not at risk posed by intensive agricultural practices. Finally, the north-south exchange we found in moth aggregation site populations was also true of moths collected throughout the Great Plains during their spring migratory period. For at least one year for each ecoregion, sampled moths were found to have high probability of origin that lay north of where they were collected. These findings better corroborate the surprising results we found above. Overall, however, evidence suggested that moth migratory patterns are largely influenced by the latitude of their origin, i.e., they typically travel within a certain latitudinal band (although not strictly along a latitudinal band, as we previously believed).

Monitoring abundance with radar

Given the paucity of moth abundance data at moth aggregation sites and our limited understanding of moth migration, we wanted to determine the viability of radar as a non-invasive method to monitor abundance and characterize the direction and speed of migrants detected. The use of radar near a moth aggregation site proved to be very effective in quantifying the amount of biomass flying overhead, and we estimate that around 5 million moths passed through the sampling plane of the radar during the 20 hours of what we assumed to be moth movement. Using this estimate to scale up to 100 km along the eastern front range of the GYE, and considering 25 nights of movement, this equates to roughly 1.2 billion moths. We were able to conclude that the densely concentrated movements of organisms in the airspace (160-750 m AGL) were most likely army cutworm moths because, per the existing literature, no other organism is migrating in such large numbers at the same time.

Management recommendations

Natal origin and feeding habits (Absaroka Range)

Because moths within the Absaroka Range came from such varied origins, it is unlikely that populations at moth aggregation sites would experience substantial declines due to regional declines within the Great Plains and prairies of Canada. Thus, this grizzly bear food source is likely not imperiled by cyclical population declines that occur within certain regions of the prairies, and we assert that there is no apparent need for management intervention. Furthermore, a proposal for the management of regions that compose the natal origin of moths would be difficult because this area likely includes Canada.

Monitoring abundance with radar

We recommend that radar should be used to monitor migrating moth populations during their spring and fall migratory period each year, ideally within 1 km of known (and accessible) moth aggregation sites, such as Peak A. These data could then be used to establish a long-term understanding of army cutworm moth abundance, and thus establish a "baseline" of abundance. Should abundance decline severely for several years, efforts to establish the cause of population declines could be mounted, and an attempt to mitigate the declines could be made.

During the spring migratory period, this monitoring effort would ideally include 25 nights, beginning in mid-June and concluding in mid-July (the timeframe known to precede peak army cutworm moth abundance). If monitoring the fall migration is feasible, we suggest that this should be conducted from mid-August to mid-September, contingent upon weather constraints. Although the fall timeframe is complicated by concurrent avian migration, it would be useful to attempt to estimate the number of moths returning the prairies. We found that the location we used to sample was easy to reach via pickup truck, but the amount of attention the radar drew from the general public was concerning—ideally, the radar could be stationed at a location for an extended period without constant surveillance.

To better characterize the relationship between the abundance of moths as estimated by the radar vs. the amount of army cutworm moths accessible to grizzly bears within the area, we suggest that density estimates established within nearby moth aggregation sites should be conducted in tandem with the first several years of the radar monitoring effort. Although the radar is able to capture migratory movement, we do not yet understand how these moths determine where to land. Direct confirmation of army cutworm moth identity via aerial sampling during these monitoring efforts should also be prioritized. (Beyond the first confirmation of army cutworm moth presence in the airspace, we think it is unlikely that these efforts will need to be repeated.)

As mentioned previously, there are several improvements that could be made in data collection moving forward. The sampling plane of the radar should also include airspace within 160 m AGL, as moth density seemed to vary inversely with increasing altitude. The addition of two radars would increase the accuracy of abundance estimates; these three radars could be stationed along 100 km of the eastern front range of the GYE. The use of lidar in concert with the radar could help validate the accuracy of abundance estimates that were made when the radar had difficulty resolving individual targets due to the density of the organisms in the airspace. Finally, examining historical and current data from the U.S. national network of WSR-88 Doppler radars for noctuid-like movements during the migratory timeframe of the army cutworm moth could be especially fruitful. Because these radars have nationwide coverage, these data could provide an ecosystem-wide understanding of army cutworm moth migration and abundance. Where we were previously limited to intra-site density estimates, our findings illustrate that radar is a viable, non-invasive means to monitor army cutworm moth populations.

REFERENCES CITED

Agostinelli, C., & Lund, U. (2017). R package ‘circular’: Circular statistics (version 0.4-93). https://r-forge.r-project.org/projects/circular/

Arritt, R. W., Rink, T. D., Segal, M., Todey, D. P., Clark, C. A., MItchell, M. J., & Labas, K. M. (1997). The Great Plains low-level jet during the warm season of 1993. *Monthly Weather Review, 125*, 2176-2192.

Augustine, D., Davidson, A., Dickinson, K., & Van Pelt, B. (2021). Thinking like a grassland: Challenges and opportunities for biodiversity conservation in the Great Plains of North America. *Rangeland Ecology & Management, 78*, 281-295.

Baker, F. S. (1944). Mountain climates of the western United States. *Ecological Monographs, 14*(2), 223-254.

Basara, J. B., Maybourn, J. N., Peirano, C. M., Tate, J. E., Brown, P. J., Hoey, J. D., & Smith, B. R. (2013). Drought and associated impacts in the Great Plains of the United States—A review.

Beerwinkle, K. R., Lopez, J. D., JR., Witz, J. A., Schleider, P. G., Eyster, R. S., & Lingren, P. D. (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, B. P. (1970). Effects of precipitation on crop insects. *The Canadian Entomologist, 102*(11), 1360-1373.

Blodgett, S. (1997). *Pheromone traps help forecast cutworm moth activity* (Montana Crop Health Report, Issue.

Blodgett, S., Lanier, W. T., & Johnson, G. D. (2003). *IPM Western Region Cutworm Survey and Risk Warning 2003 Report*. Montana State University. http://scarab.msu.montana.edu/Cutworm/CW2003.htm

Bowen, G. J., Ehleringer, J. R., Chesson, L. A., Stange, E., & Cerling, T. E. (2007). Stable isotope ratios of tap water in the contiguous United States. *Water Resources Research, 43*(3).

Bowen, G. J., Wassenaar, L. I., & Hobson, K. A. (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia, 143*(3), 337-348.

Brattström, O., Bensch, S., Wassenaar, L. I., Hobson, K. A., & Åkesson, S. (2010). Understanding the migration ecology of European red admirals Vanessa atalanta using stable hydrogen isotopes. *Ecography, 33*(4), 720-729.

Brower, L. P., Taylor, O. R., Williams, E. H., Slayback, D. A., Zubieta, R. R., & Ramirez, M. I. (2012). Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity, 5*(2), 95-100.

Burton, R. L., Starks, K., & Peters, D. (1980). The Army Cutworm. *Oklahoma Agricultural Experiment Station*(Bulletin No. B749).

Carter, P. R., Hicks, D. R., Oplinger, E. S., Doll, J. D., Bundy, L. G., Schuler, R. T., & Holmes, B. J. (1989). Grain Sorghum (Milo). *Alternative Field Crops Manual*.

Chapman, J. A., Romer, J. I., & Stark, J. (1955). Ladybird beetles and army cutworm adults as food for grizzly bears in Montana. *Ecology, 36*(1), 156-158.

Chapman, J. W., Drake, V. A., & Reynolds, D. R. (2011). Recent insights from radar studies of insect flight. *Annual Review of Entomology, 56*, 337-356.

Chapman, J. W., Nesbit, R. L., Burgin, L. E., Reynolds, D. R., Smith, A. D., Middleton, D. R., & Hill, J. K. (2010). Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science, 327*(5966), 682-685.

Chapman, J. W., Reynolds, D. R., & Smith, A. D. (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, J. W., Reynolds, D. R., & Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecology letters, 18*(3), 287-302.

Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology, 18*(19), R908-R909.

Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008a). A seasonal switch in compass orientation in a high-flying migrant moth. *Current Biology, 18*(19), R908-R909.

Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology, 18*(7), 514-518.

Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., Smith, A. D., & Woiwod, I. P. (2008b). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology, 18*(7), 514-518.

Choate, C. M. (1963). *Ordination of the Alpine plant communities at Logan Pass Glacier National Park Montana* Montana State University].

Common, I. (1954). A study of the ecology of the adult bogong moth, Agrotis infusa (Boisd)(Lepidoptera: Noctuidae), with special reference to its behaviour during migration and aestivation. *Australian journal of zoology, 2*(2), 223-263.

Cook, W. C. (1927). Studies in the ecology of Montana cutworms (Phalaenidae). *Ecology, 8*, 158-173.

Cooley, R. A. (1916). Observations on the life history of the army cutworm, Chorizagrotis auxiliaris. *J. Agric. Res, 6*, 871-881.

Coop, J. D., Hibner, C. D., Miller, A. J., & Clark, G. H. (2005). Black bears forage on army cutworm moth aggregations in the Jemez Mountains, New Mexico. *The Southwestern Naturalist, 50*(2), 278-281.

Crum, T. D., & Alberty, R. L. (1993). The WSR-88D and the WSR-88D operational support facility. *Bulletin of the American Meteorological Society, 74*(9), 1669-1688.

Damm, C. (2001). *A Phytosociological Study of Glacier National Park, Montana, U.S.A., with Notes on the Syntaxonomy of Alpine Vegetation in Western North America* Georg-August-Universität zu Göttingen].

Dirks, R. A., & Martner, B. E. (1982). *The climate of Yellowstone and Grand Teton National Parks*. US Department of the Interior, National Park Service.

Endler, J. A. (1973). Gene flow and population differentiation. *Science, 179*, 243-250.

Finklin, A. I. (1986). *A Climatic Handbook for Glacier National Park: With Data for Waterton Lakes National Park* (Vol. 204). US Department of Agriculture, Forest Service, Intermountain Research Station.

Flockhart, D. T., Brower, L. P., Ramirez, M. I., Hobson, K. A., Wassenaar, L. I., Altizer, S., & Norris, D. R. (2017). Regional climate on the breeding grounds predicts variation in the natal origin of monarch butterflies overwintering in Mexico over 38 years. *Global change biology, 23*(7), 2565-2576.

Fortin, J. K., Schwartz, C. C., Gunther, K. A., Teisberg, J. E., Haroldson, M. A., Evans, M. A., & Robbins, C. T. (2013). Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of Wildlife Management, 77*(2), 270-281.

French, S. P., French, M. G., & Knight, R. R. (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, C. P. (1903). *Some of the more important insects of 1903* (Vol. 94). Bulletin of the Colorado Agriculture Experiment Station

Gunther, K. A., Shoemaker, R. R., Frey, K. L., Haroldson, M. A., Cain, S. L., Van Manen, F. T., & Fortin, J. K. (2014). Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus*, 61-73.

Hardwick, D., & Lefkovitch, L. (1971). Physical and biotic factors affecting Euxoa species abundance in western North America: a regression analysis. *The Canadian Entomologist, 103*(9), 1217-1235.

Heinrich, K., & Collins, L. (2017). Determining the geographical origin of Asian longhorn beetle (Anoplophora glabripennis) specimens using stable isotope and trace element analyses. *Pest management science, 73*(5), 967-975.

Hendrix III, W., Mueller, T., Phillips, J., & Davis, O. (1987). Pollen as an indicator of long-distance movement of Heliothis zea (Lepidoptera: Noctuidae). *Environmental entomology, 16*(5), 1148-1151.

Hobson, K. A., & Norris, D. R. (2008). *Animal migration: a context for using new techniques and approaches. Tracking animal migration with stable isotopes*. Academic Press.

Hobson, K. A., & Wassenaar, L. I. (2019). *Tracking animal migration with stable isotopes*. Academic Press.

Hobson, K. A., Doward, K., Kardynal, K. J., & McNeil, J. N. (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.

Hobson, K. A., Kusack, J. W., Gootgarts, J., Longstaffe, F. J., & McNeil, J. N. (2022). Using stable isotopes (δ 2H, δ 13C) to identify natal origins and larval host plant use by western bean cutworm, Striacosta albicosta (Lepidoptera: Noctuidae) captured in southern Ontario. *Ecological Entomology*.

Hobson, K. A., Soto, D. X., Paulson, D. R., Wassenaar, L. I., & Matthews, J. H. (2012). A dragonfly (δ2H) isoscape for North America: a new tool for determining natal origins of migratory aquatic emergent insects. *Methods in ecology and evolution, 3*(4), 766-772.

Hobson, K. A., Wassenaar, L. I., & Taylor, O. R. (1999, 1999/08/01). Stable isotopes (δD and δ13C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia, 120*(3), 397-404. https://doi.org/10.1007/s004420050872

Hobson, K., Wassenaar, L. I., Mila, B., Lovette, I., Dingle, C., & Smith, T. B. (2003). Stable isotope as indicators of altitudinal distributions and moevments in an Ecuadorean hummingbird community. *Oecologia, 136*, 302-308.

Holder, P. W., Armstrong, K., Van Hale, R., Millet, M.-A., Frew, R., Clough, T. J., & Baker, J. A. (2014). Isotopes and trace elements as natal origin markers of Helicoverpa armigera–an experimental model for biosecurity pests. *PloS one, 9*(3), e92384.

Hu, G., Lim, K. S., Horvitz, N., Clark, S. J., Reynolds, D. R., Sapir, N., & Chapman, J. W. (2016). Mass seasonal bioflows of high-flying insect migrants. *Science, 354*(6319), 1584-1587.

Hyodo, F. (2015). Use of stable carbon and nitrogen isotopes in insect trophic ecology. *Entomological Science, 18*(3), 295-312.

Jacobson, L. A., & Blakeley, P. E. (1959). Development and behavior of the army cutworm in the laboratory. *Annals of the Entomological Society of America, 52*(1), 100-105.

Johnson, S. A. (1905). Cutworms. *Colorado Experiment Station Bulletin, No. 98.*

Kendall, D. M. (1981). *Bionomics of Euxoa auxiliaris Grote (Lepidoptera: Noctuidae) in the Rocky Mountains and comparison with two resident species of alpine moths* University of Colorado (at Colo. Spgs.].

Kendall, D. M., Kevan, P. G., & LaFontaine, J. D. (1981). Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist, 113*(7), 607-614.

Kevan, P. G., & Kendall, D. M. (1997, 1997/11/01). 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://doi.org/10.1080/00040851.1997.12003268

Koel, T. M., Bigelow, P. E., Doepke, P. D., Ertel, B. D., & Mahony, D. L. (2005). Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries, 30*(11), 10-19.

Koerwitz, F., & Pruess, K. (1964). Migratory potential of the army cutworm. *Journal of the Kansas Entomological Society, 37*(3), 234-239.

Kucharik, C. J. (2006). A multidecadal trend of earlier corn planting in the central USA. *Agronomy Journal, 98*(6), 1544-1550.

Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., Kruk, M. C., Thomas, D., Shulski, M., & Umphlett, N. A. (2013). Regional climate trends and scenarios for the US National Climate Assessment Part 4. Climate of the US Great Plains.

Lafontaine, J. (1987). *The Moths of North America North of Mexico. Fascicle 27.2. Noctuoidea Noctuidae (Part)*. The Wedge Entomological Foundation Washington.

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., & Yeager, L. A. (2012). Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological reviews, 87*(3), 545-562.

Lincoln, F. C. (1935). *The migration of North American birds*. US Department of Agriculture.

Ma, C., Vander Zanden, H. B., Wunder, M. B., & Bowen, G. J. (2020). assignR: An r package for isotope-based geographic assignment. *Methods in ecology and evolution, 11*(8), 996-1001.

Manen, F. T. v., Haroldson, M. A., Bjornlie, D. D., Erbinger, M. R., Thompson, D. J., Costello, C. M., & White, G. C. (2016). Density Dependence, Whitebark Pine, and Vital Rates of Grizzly Bears. *The Journal of Wildlife Management, 80*(2), 300-313.

Mani, M. S. (1962). *Introduction to High Altitude Entomology*. Methuen & Co.

Mani, M. S. (1968). *Ecology and biogeography of high altitude insects* (Vol. 4). Springer Science & Business Media.

Marshall, J. D., Brooks, J. R., & Lajtha, K. (2007). *Sources of variation in the stable isotopic composition of plants*. Blackwell.

Marston, R. A., & Anderson, J. E. (1991). Watersheds and vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology, 5*(3), 338-346.

Mattson, D. J., Gillin, C. M., Benson, S. A., & Knight, R. R. (1991). Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology, 69*(9), 2430-2435.

May, M. L. (2013). A critical overview of progress in studies of migration of dragonflies (Odonata: Anisoptera), with emphasis on North America. *Journal of Insect Conservation, 17*(1), 1-15.

McNabb, D. M., Halaj, J., & Wise, D. H. (2001). Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. *Pedobiologia, 45*(4), 289-297.

Middleton, A. D., Sawyer, H., Merkle, J. A., Kauffman, M. J., Cole, E. K., Dewey, S. R., Gude, J. A., Gustine, D. D., McWhirter, D. E., & Proffitt, K. M. (2020). Conserving transboundary wildlife migrations: recent insights from the Greater Yellowstone Ecosystem. *Frontiers in Ecology and the Environment, 18*(2), 83-91.

Morrill, W. (1991). Montana small grain insects: armyworms and cutworms. *Montana Agriculture Experiment Station, Montana State University, Bozeman, Capsule Information Ser*(34).

Nelson, A. A., Kauffman, M. J., Middleton, A. D., Jimenez, M. D., McWhirter, D. E., & Gerow, K. (2016). Native prey distribution and migration mediates wolf (Canis lupus) predation on domestic livestock in the Greater Yellowstone Ecosystem. *Canadian Journal of Zoology, 94*(4), 291-299.

Nelson, R. A., Folk Jr, G. E., Pfeiffer, E. W., Craighead, J. J., Jonkel, C. J., & Steiger, D. L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management*, 284-290.

Nunlist, E. (2020). *Grizzly Bears and Humans at Two Moth Aggregation Sites in Wyoming* Montana State University]. Bozeman, Montana.

Nussbaumer, R., Schmid, B., Bauer, S., & Liechti, F. (2021). A Gaussian mixture model to separate birds and insects in single-polarization weather radar data. *Remote Sensing, 13*(10), 1989.

O'Brien, S. L., & 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.

O'Brien, S. L., & Lindzey, F. G. (1998). Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus*, 427-435.

Oku, T., Chiba, T., & Fuse, H. (1983). Phenology and behaviour of cutworms, *Euxoa sibirica* Boisduval and *E. oberthueri* Butler (Lepidoptera, Noctuidae), in Tohoku district: II. Seasonal trap catches of adults in relation to aestival diapause and migration. *Kontyû, 51*, 144-157.

Oku, T., Saito, O., Fuse, H., & Chiba, T. (1982). Phenology and behavior of cutowrms, *Euxoa sibirica* Boisduval and *E. oberthueri* Buter (Lepidoptera, Noctuidae), in Tohoku district: I. Seasonal trap cataches of adults in relation to aestival diapause and migration. *Kontyû, 50*, 301-313.

Omernik, J. M., & Griffith, G. E. (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environmental management, 54*(6), 1249-

Pardo, L. H., & Nadelhoffer, K. J. (2010). Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. In *Isoscapes* (pp. 221-249). Springer.

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.

Pogue, M. G., & Simmons, R. B. (2008). A new pest species of Copitarsia (Lepidoptera: Noctuidae) from the neotropical region feeding on Asparagus and cut flowers. *Annals of the Entomological Society of America, 101*(4), 743-762.

Ponsard, S., Bethenod, M.-T., Bontemps, A., Pélozuelo, L., Souqual, M.-C., & Bourguet, D. (2004). Carbon stable isotopes: a tool for studying the mating, oviposition, and spatial distribution of races of European corn borer, Ostrinia nubilalis, among host plants in the field. *Canadian Journal of Zoology, 82*(7), 1177-1185.

Prasifka, J., & Heinz, K. (2004). The use of C3 and C4 plants to study natural enemy movement and ecology, and its application to pest management. *International Journal of Pest Management, 50*(3), 177-181.

Pruess, K. P., & Pruess, N. C. (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.

Pruess, K., & Pruess, N. C. (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.

Quinby, B. M., Creighton, J. C., & Flaherty, E. A. (2020). Stable isotope ecology in insects: a review. *Ecological Entomology, 45*(6), 1231-1246.

Reynolds, D., & Riley, J. (1997). *Flight behaviour and migration of insect pests. Radar studies in developing countries*. Natural Resources Institute (NRI).

Robinson, E. B., & Dietz, J. L. (2020). *Great Plains*. https://www.britannica.com/place/Great-Plains

Robison, H. L. (2009). *Relationships between Army Cutworm Moths and Grizzly Bear Conservation* University of Nevada, Reno].

Robison, H. L., Schwartz, C. C., Petty, J. D., & Brussard, P. F. (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.

Rosenberg, N. J. (1987). Climate of the Great Plains region of the United States. *Great Plains Quarterly*, 22-32.

Schaefer, G. (1969). Radar studies of locust, moth and butterfly migration in the Sahara. *Proc Royal Entomol Soc Lond C, 34*(33), 39-40.

Schwartz, C. C., Fortin, J. K., Teisberg, J. E., Haroldson, M. A., Servheen, C., Robbins, C. T., & Van Manen, F. T. (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.

Seamans, H. (1928). Forecasting Outbreaks of the Army Cutworm (Chonzagrotis auxiliaris, Grote). *Forecasting Outbreaks of the Army Cutworm (Chonzagrotis auxiliaris, Grote).*

Shapiro, A., & Fedorovich, E. (2008). Coriolis effects in homogeneous and inhomogeneous katabatic flows. *Quarterly Journal of the Royal Meteorological Society, 134*.

Shapiro, A., Fedorovich, E., & Rahimi, S. (2016). A Unified Theory for the Great Plains Nocturnal Low-Level Jet. *Journal of Atmospheric Sciences, 73*, 3037-3057.

Showers, W. B., Smelser, R. B., Keaster, A. J., Whitford, F., Robinson, J. F., Lopez, J. D., & Taylor, S. E. (1989a). Recapture of marked black cutworm (Lepidoptera: Noctuidae) males after long-range transport. *Environmental entomology, 18*(3), 447-458.

Showers, W. B., Whitford, F., Smelser, R. B., Keaster, A. J., Robinson, J. F., Lopez, J. D., & Taylor, E. S. (1989). Direct Evidence for Meteorologially Driven Long-Range Dispersal of an Economically Important Moth. *Ecology, 70*, 987-992.

Snow, S. J. (1925). Observations on the cutworm, *Euxoa auxiliaris* Grote, and its principal parasites. *Journal of Economic Entomology, 18*(4), 602-609.

Song, J., Liao, K., Coulter, R. L., & Lesht, B. M. (2005). Climatology of the low-level jet at the Southern Great Plains Atmospheric Boundary Layer Experiments site. *Journal of Applied Meteorology 44*, 1593-1606.

Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016). Long-distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology letters, 12*(10), 20160561.

Stepanian, P. M., Entrekin, S. A., Wainwright, C. E., Mirkovic, D., Tank, J. L., & Kelly, J. F. (2020). Declines in an abundant aquatic insect, the burrowing mayfly, across major North American waterways. *Proceedings of the National Academy of Sciences, 117*(6), 2987-2992.

Strickland, E. H. (1916). *The Army Cutworm: Euxoa (Chorizagrotis) Auxiliaris Grote* (Vol. Bulletin 13). Canadian Department of Agricultural Entomology.

Sundell, K. A. (1993). *Geology of Wyoming: Geological Survey of Wyoming Memoir No. 5*.

Team, R. C. (2020). *R: A language and environment for statistical computing.* In R Foundation for Statistical Computing. https://www.R-project.org/

Terzer, S., Wassenaar, L. I., Araguás-Araguás, L. J., & Aggarwal, P. K. (2013). Global isoscapes for δ18O and δ2H in precipitation: improved prediction using regionalized climatic regression models. *Hydrology and Earth System Sciences, 17*(11), 4713-4728. https://doi.org/10.5194/hess-17-4713-2013

Terzer, S., Wassenaar, L. I., Araguás-Araguás, L. J., & Aggarwal, P. K. (2013). Global isoscapes for δ18O and δ2H in precipitation: improved prediction using regionalized climatic regression models. *Hydrology and Earth System Sciences, 17*(11), 4713-4728. https://doi.org/10.5194/hess-17-4713-2013
the natal origins and wing morphology of overwintering western monarch butterflies.

Thilenius, J. F., & Smith, D. R. (1985). Vegetation and soils of an alpine range in the Absaroka Mountains, Wyoming. *US Dept of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station*, 1-23.

Triplehorn, C. A., Johnson, N. F., & Borror, D. J. (2005). *Borror and DeLong's Introduction to the Study of Insects*.

University of Nebraska, L. (2020). *Light Trap Data*. https://entomology.unl.edu/fldcrops/lightrap

USDA. (1951-1975). Cooperative Economic Insect Report.

USDA. (2022). *United States — Crop Production Maps*. https://ipad.fas.usda.gov/rssiws/al/us_cropprod.aspx

USFS. (2007). Final conservation strategy for the grizzly bear in the Greater Yellowstone Area.

USFS. (2015). Land Management Plan 2015 Revision.

Waddington, J. C., & Wright, H. (1974). Late Quaternary Vegetational Changes on the East Side of Yellowstone Park, Wyoming1. *Quaternary Research, 4*(2), 175-184.

Walkden, H. H. (1942). *Owlet moths (Phalaenidae) taken at light traps in Kansas and Nebraska*. US Department of Agriculture.

Walkden, H. H. (1950). *Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains*.

Walters, C. K., Winkler, J. A., Shadbolt, R. P., Ravensway, J. v., & Bierly, G. D. (2008). A long-term climatology of southerly and northerly low-level jets for the central United States. *Annals of the American Association of Geographers, 98*, 521-552.

Warrant, E., Frost, B., Green, K., Mouritsen, H., Dreyer, D., Adden, A., Brauburger, K., & Heinze, S. (2016). The Australian Bogong moth Agrotis infusa: a long-distance nocturnal navigator. *Frontiers in Behavioral Neuroscience, 10*, 77.

Wassenaar, L. (2009). *Manual for the Use of Stable Isotopes in Entomology*. International Atomic Energy Agency.

Wassenaar, L. I., & Hobson, K. A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences, 95*(26), 15436-15439.

Wassenaar, L. I., & Hobson, K. A. (2000). Improved method for determining the stable-hydrogen isotopic composition (dD) of complex organic materials of environmental interest. *Environmental Science and Technology, 34*, 2354-2360.

Wassenaar, L. I., & Hobson, K. A. (2003). Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopic in Environmental and Health Studies, 39*.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution, 17*(2), 76-83.

West, J. B., Bowen, G. J., Cerling, T. E., & Ehleringer, J. R. (2006). Stable isotopes as one of nature's ecological recorders. *Trends in Ecology & Evolution, 21*(7), 408-414.

West, J. B., Bowen, G. J., Dawson, T. E., & Tu, K. P. (2009). *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer.

Westbrook, J. K. (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

Westbrook, J., & Wolf, W. (1998). Migratory flights of bollworms, Helicoverpa zea (Boddie), indicated by Doppler weather radar. Preprints-Weather Data Requirements for Integrated Pest Management: 23rd Conference on Agricultural and Forest Meteorology, 2nd Urban Environment Symposium, and 13th Conference on Biometeorology and Aerobiology,

White, D. D. (1996). *Two grizzly bear studies: moth feeding ecology and male reproductive biology* [PhD, Montana State University-Bozeman, College of Letters & Science].

White, D. D. K., K.C..; and Picton, H.D. (1999). Potential Energetic Effects of Mountain Climbers on Foraging Grizzly Bears. *Wildlife Society Bulletin (1973-2006), 27*, 146-151.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998a). Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology, 76*(2), 221-227.

White, J., Don, Kendall, K. C., & Picton, H. D. (1998b). Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana. *Canadian Journal of Zoology, 76*(5), 835-842.

Willis, B. (1902). Stratigraphy and structure, Lewis and Livingston ranges, Montana. *Bulletin of the Geological Society of America, 13*(1), 305-352.

Wood, C. R., Chapman, J. W., Reynolds, D. R., Barlow, J. F., Smith, A. D., & Woiwod, I. P. (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.

Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In *Isoscapes* (pp. 251-270). Springer.

Yang, L. H., Ostrovsky, D., Rogers, M. C., & Welker, J. M. (2016). Intra-population variation in the natal origins and wing morphology of overwintering western monarch butterflies *Danaus plexippus*. *Ecography*, *39*(10), 998-1007.

APPENDICES

APPENDIX A

SPRING AND FALL ARMY CUTWORM MOTH COLLECTION

Table 9: Spring army cutworm moth (*Euxoa auxiliaris*) collection efforts detailing the county/state, year of collection, and number of samples collected (2018-2021).

County_state	Year	*n*
Albany_WY	2020	30
Albany_WY	2021	30
Beaver_UT	2019	1
Bernalillo_NM	2019	76
Bernalillo_NM	2021	3
Bingham_ID	2020	1
Bonneville_ID	2018	4
Bonneville_ID	2019	15
Bonneville_ID	2020	15
Bonneville_ID	2021	11
Cascade_MT	2020	2
Clay_NE	2018	7
Clay_NE	2019	3
Clay_NE	2020	42
Clay_NE	2021	29
Dawes_NE	2020	29
Eddy_NM	2020	22
FallRiver_SD	2020	9
Finney_KS	2019	5
Finney_KS	2021	20
Gallatin_MT	2019	2
Gallatin_MT	2020	18
Gallatin_MT	2021	5
Garden_NE	2018	5
Grand_UT	2020	2
Hughes_SD	2020	13
Keith_NE	2018	2
Laramie_WY	2018	4
Larimer_CO	2020	31
Lincoln_CO	2019	26
Lincoln_NE	2018	16
Lincoln_NE	2019	12
Lincoln_NE	2020	30
Lincoln_NE	2021	24
McKenzie_ND	2021	2

Table 9 Continued

County_state	Year	*n*
Mesa_CO	2020	3
Missoula_MT	2020	29
Morgan_CO	2019	13
Park_WY	2019	11
Park_WY	2020	54
Pennington_SD	2020	29
Platte_NE	2020	17
Platte_WY	2018	2
Quay_NM	2020	30
Richland_MT	2020	56
Rosebud_MT	2020	30
Rosebud_MT	2021	18
SaltLake_UT	2018	3
Scottsbluff_NE	2018	9
Scottsbluff_NE	2019	5
Scottsbluff_NE	2020	27
Sublette_WY	2019	16
Washakie_WY	2018	3
Washakie_WY	2019	5
Washakie_WY	2020	10
Weld_CO	2019	3
Williams_ND	2020	21

Table 10: Fall army cutworm moth (*Euxoa auxiliaris*) collection efforts detailing the county/state, year, and number of samples collected (2020-2021).

County_State	Year	*n*
Albany_WY	2020	34
Bonneville_ID	2020	15
Cache_UT	2020	4
Clay_NE	2020	51
ClearCreek_CO	2020	26
Finney_KS	2020	46
Gallatin_MT	2021	5
Madison_MT	2020	8
Missoula_MT	2021	9
Pennington_SD	2021	30
Richland_MT	2020	34
Richland_MT	2021	30

Table 10 Continued

County_State	Year	*n*
Wall_SD	2021	1

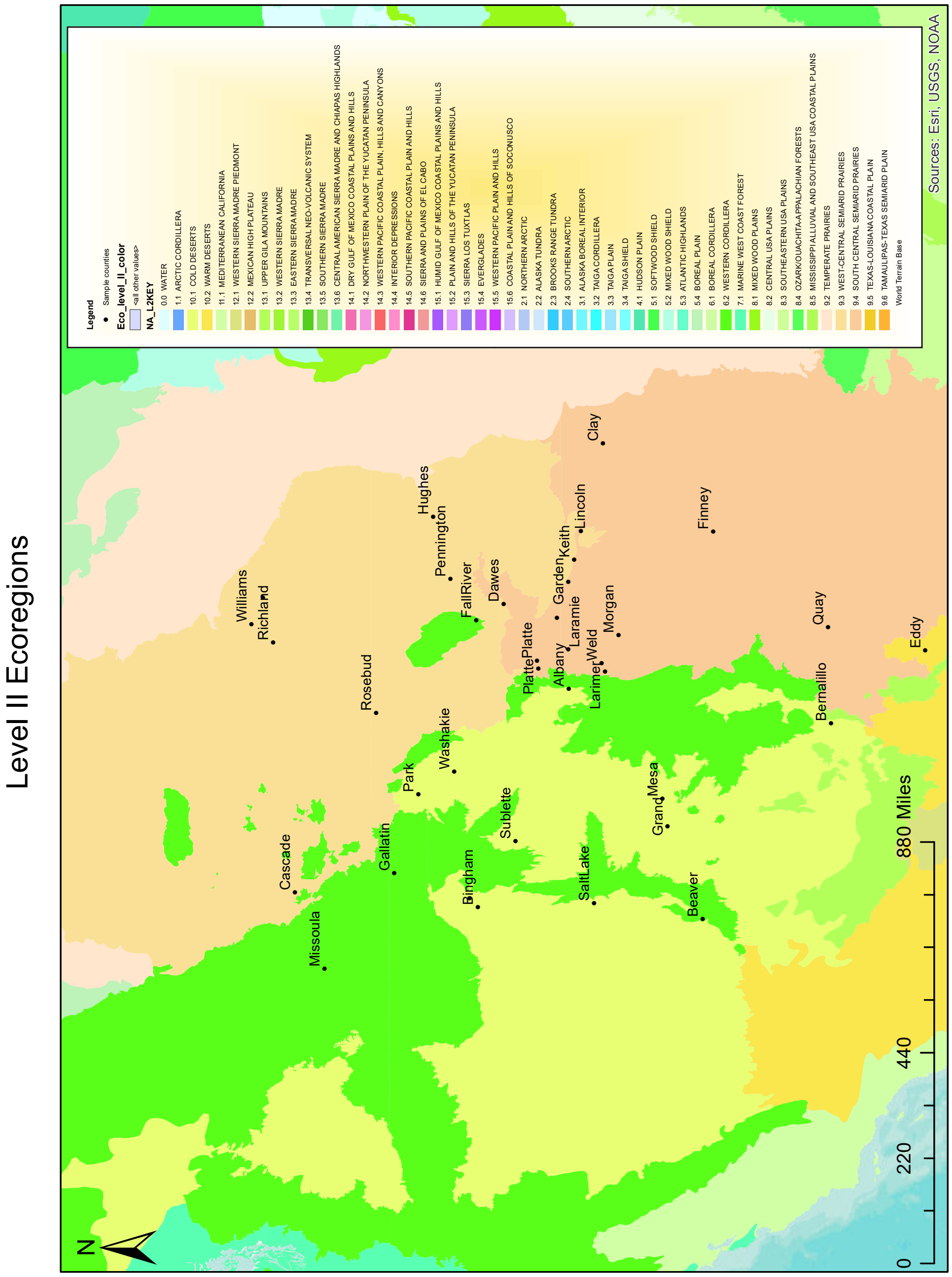


Figure 21: Map of counties throughout the Great Plains, and the ecoregions into which the counties fall, in which army cutworm moths (*Euxoa auxiliaris*) were collected from 2018-2021 during the spring and fall migratory period.

APPENDIX B

SUPPLEMENTARY UNION PROBABILITY MAPS

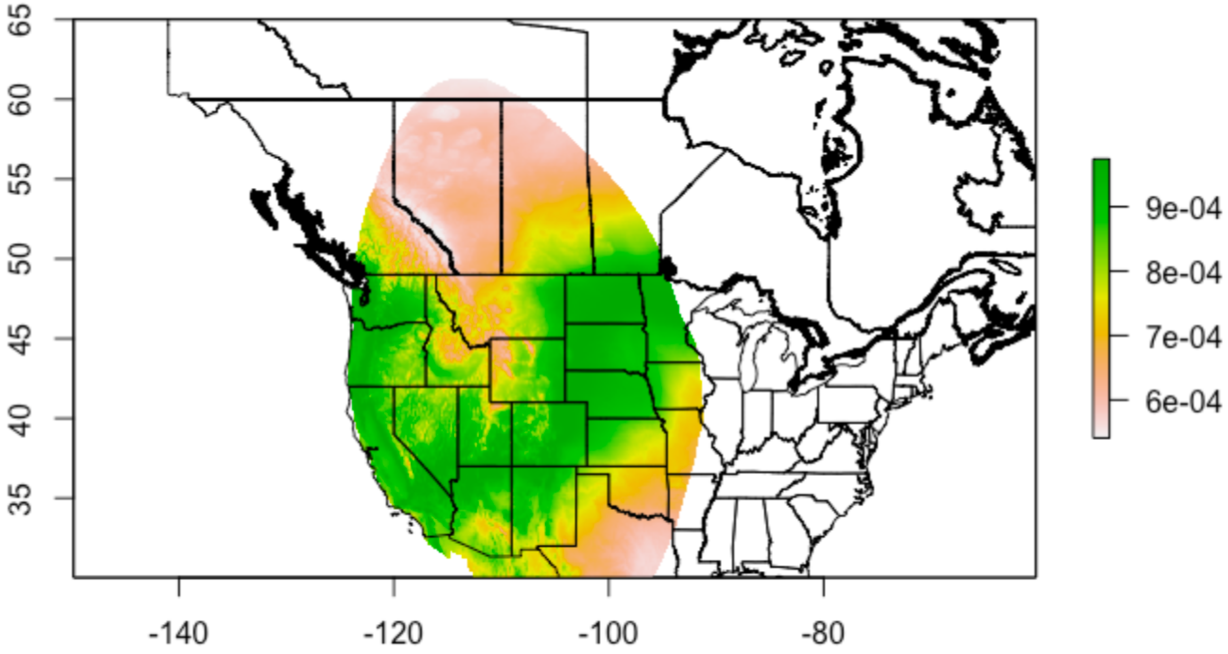


Figure 22: Union probability, the probability that any sample originated from each grid cell within the isoscape, calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the south-central semiarid prairies in the spring of 2018, 2019, and 2020 (*n* = 96).

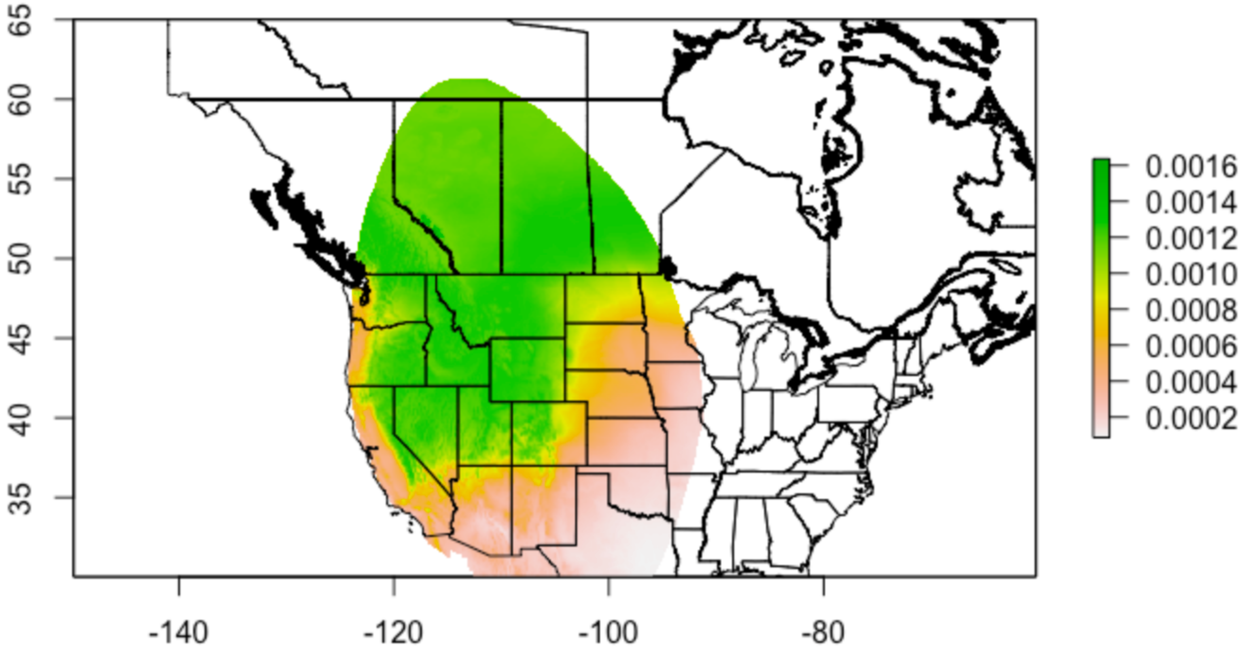


Figure 23: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the south-central semiarid prairies in the spring of 2021 (*n* = 103).

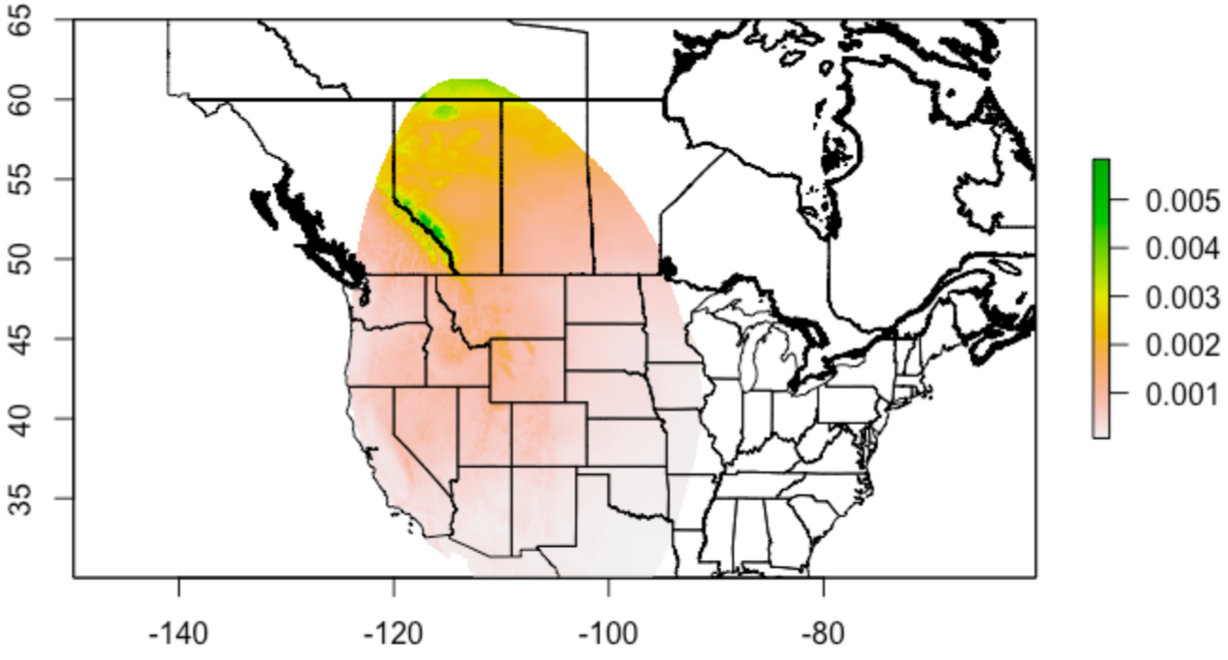


Figure 24: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the western cordillera in the spring of 2018—2021 (*n* = 100).

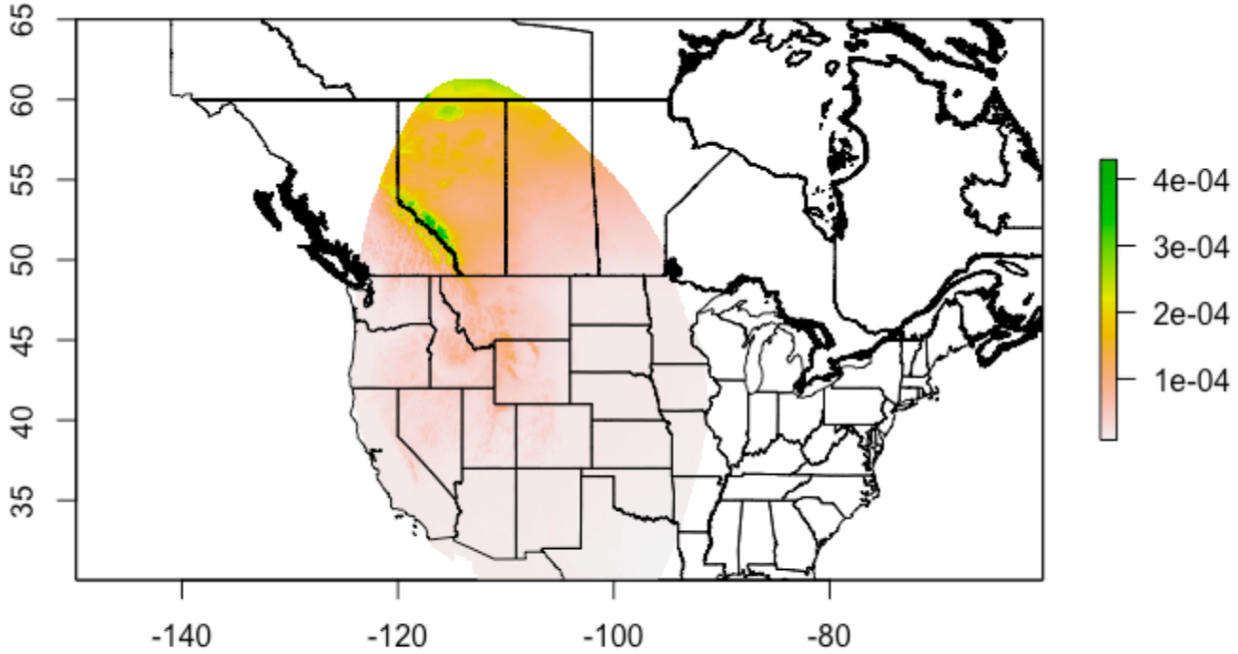


Figure 25: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the cold deserts in the spring of 2018 (n = 6).

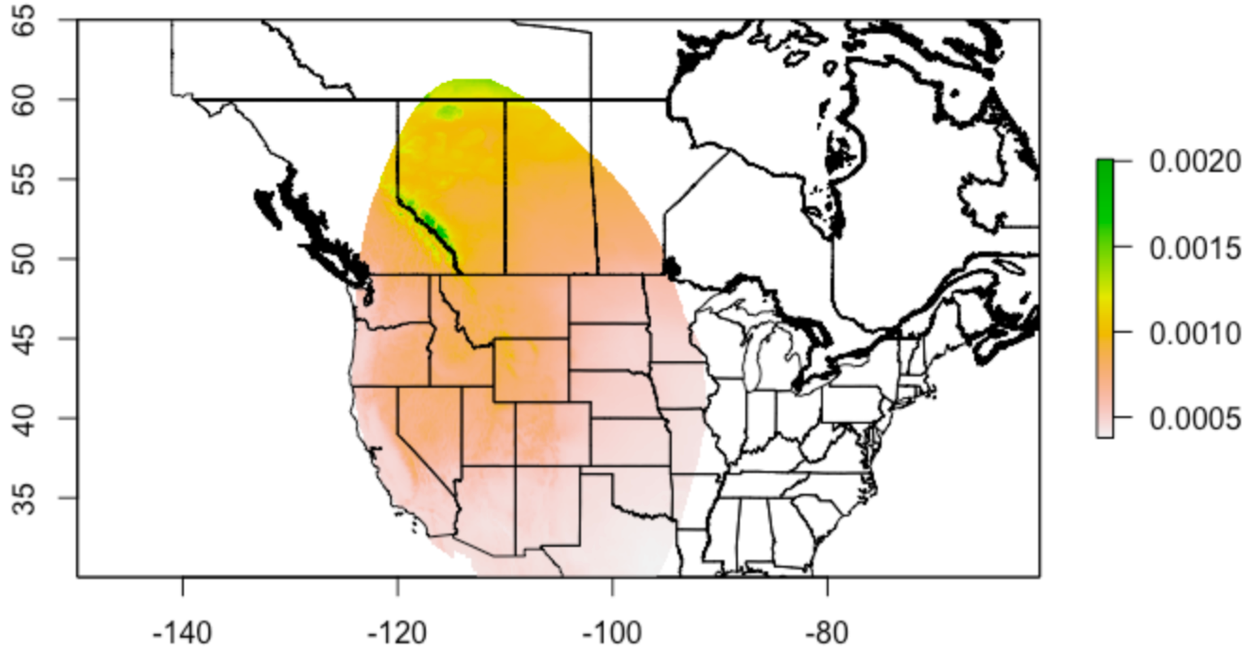


Figure 26: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the cold deserts in the spring of 2019, 2020, and 2021 (n = 83).

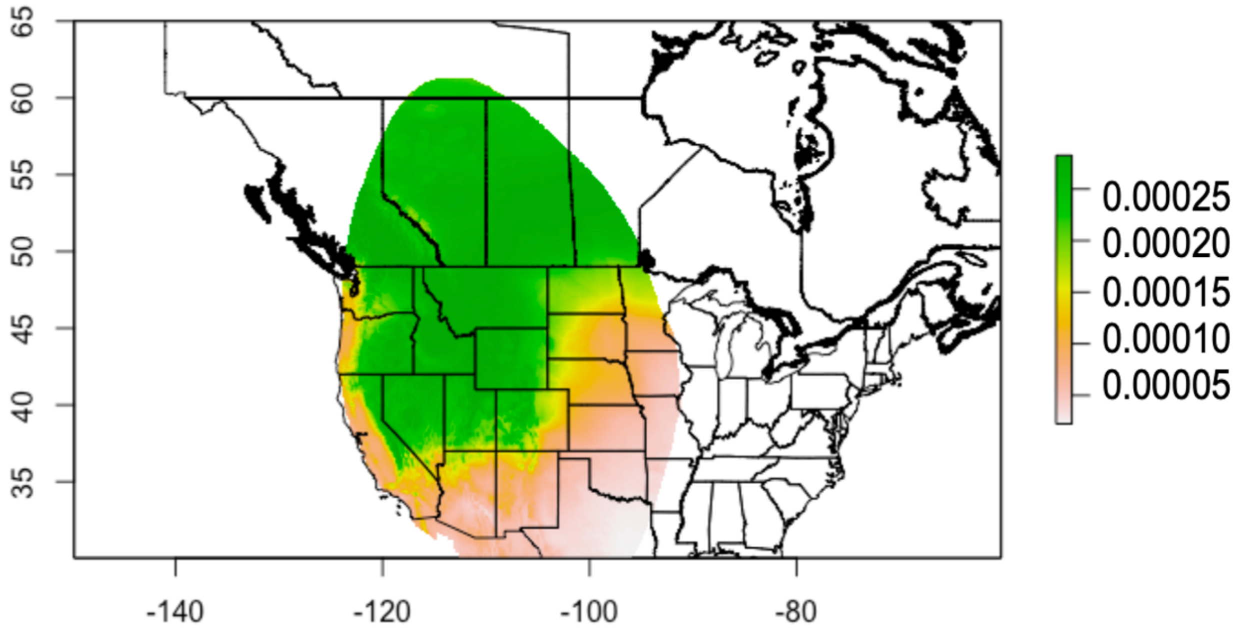


Figure 27: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the warm deserts in the spring of 2020 (n = 22).

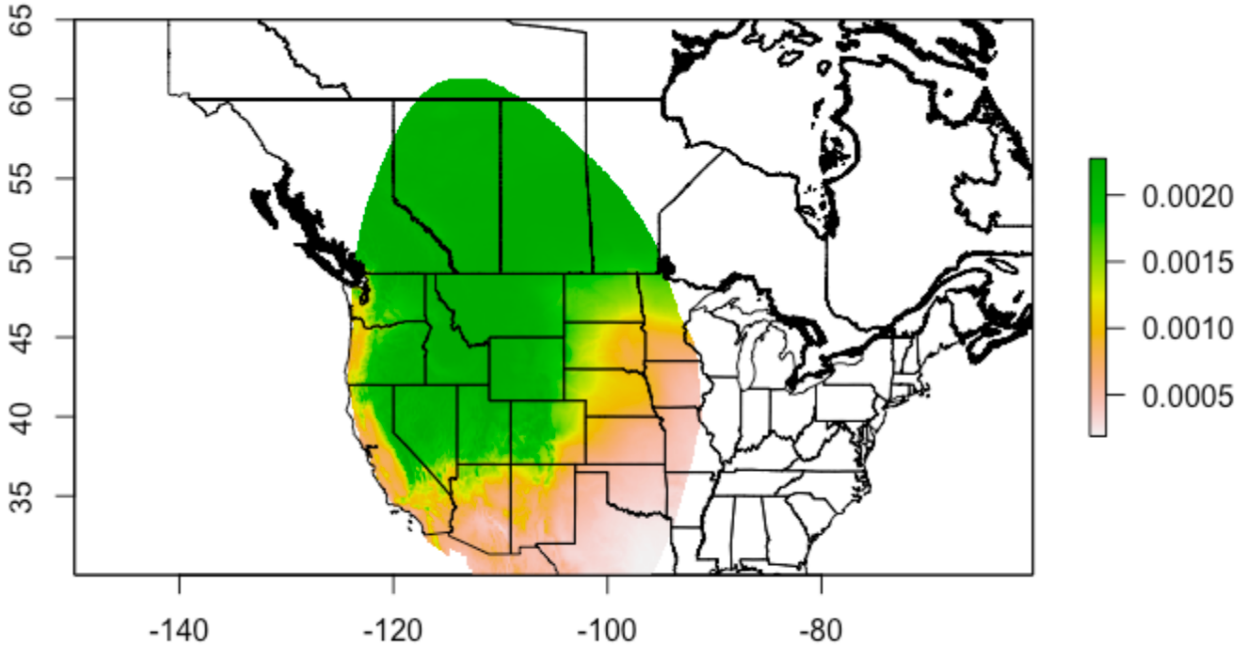


Figure 28: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the west-central semiarid prairies in the spring of 2020 (n = 188).

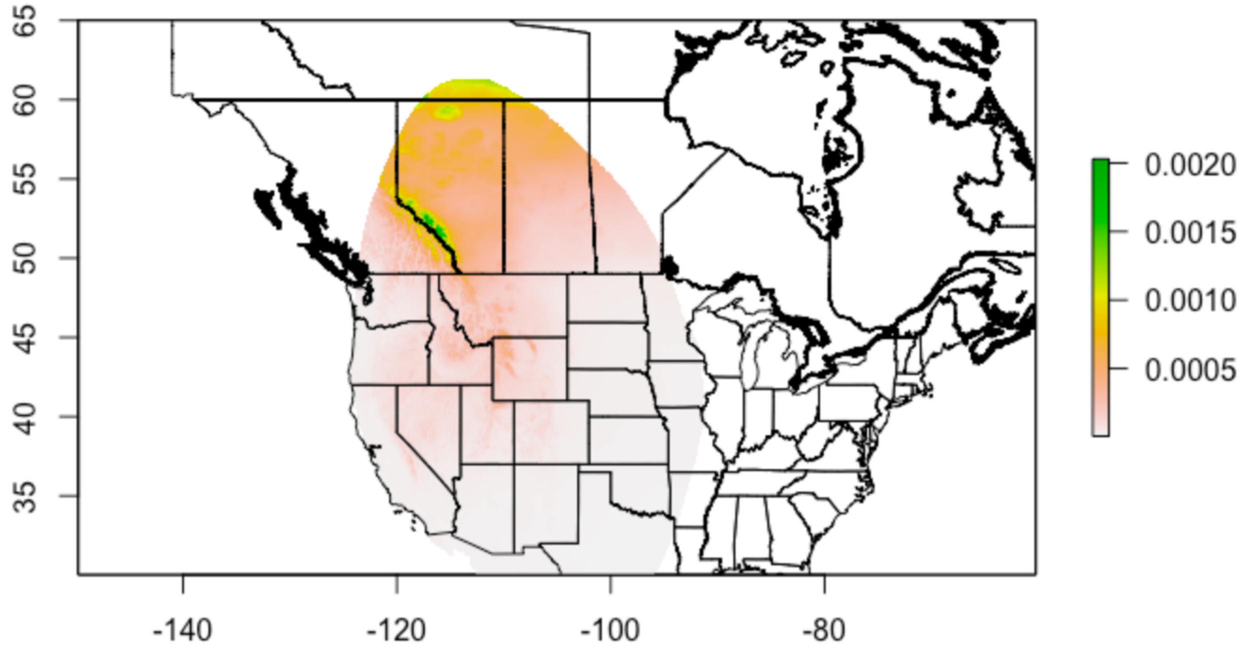


Figure 29: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the west-central semiarid prairies in the spring of 2021 ($n = 20$).

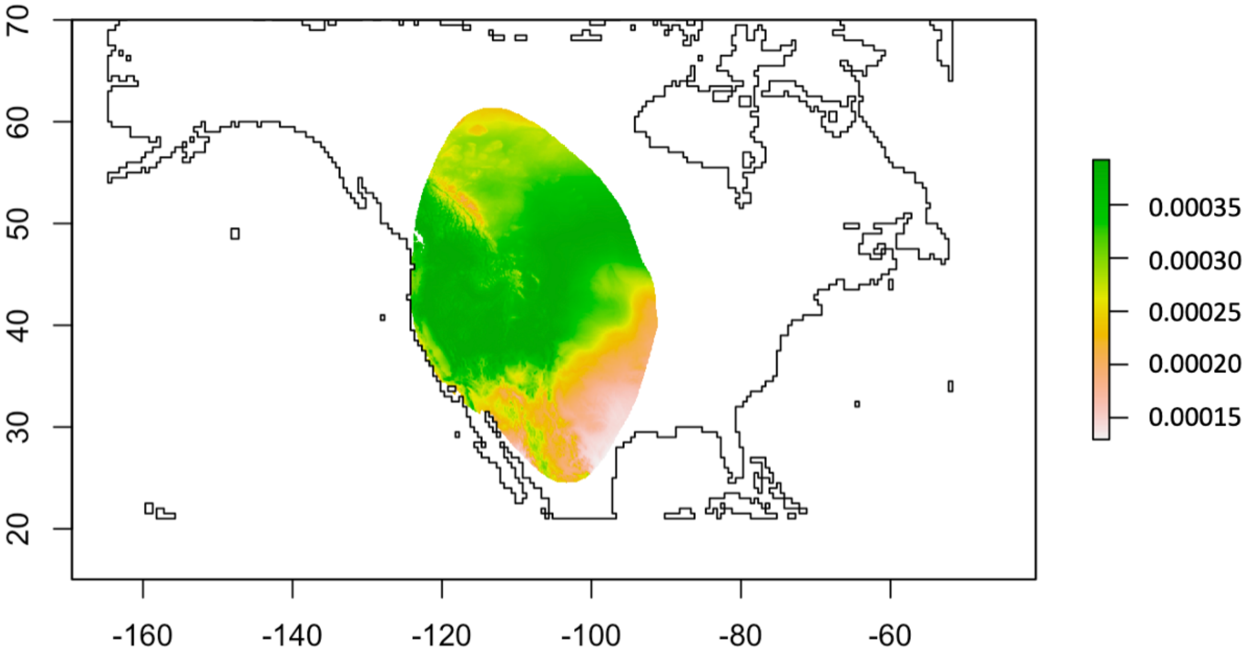


Figure 30: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the cold deserts in the fall of 2020 ($n = 38$).

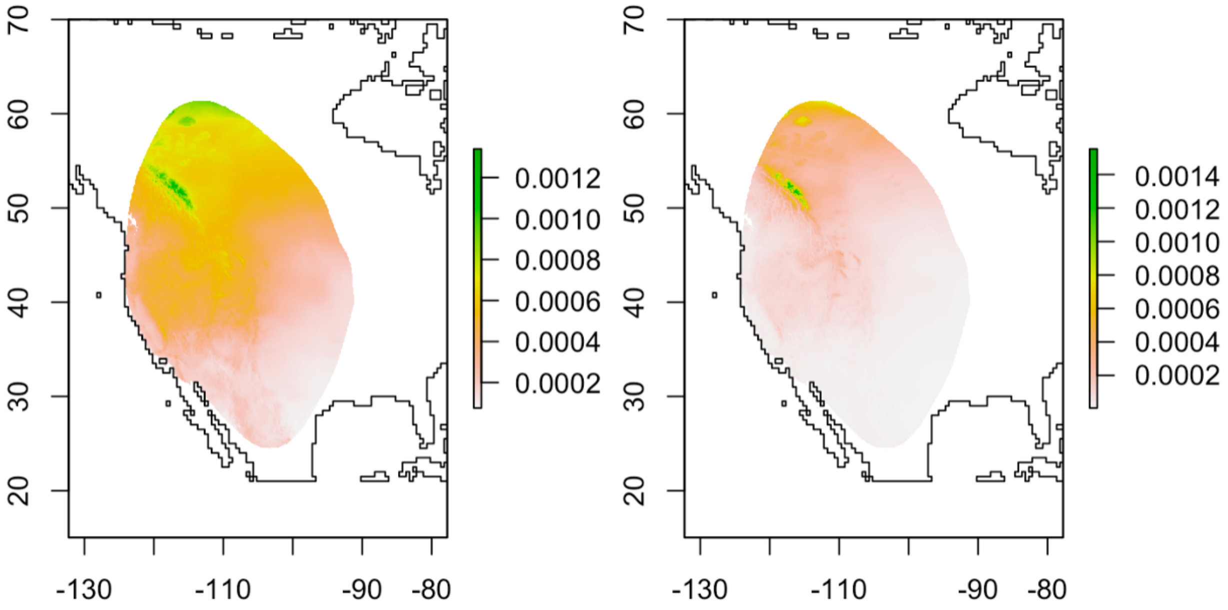


Figure 31: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the western cordillera ecoregion in the fall of 2020 (left, *n* = 49) and 2021 (right; *n* = 14).

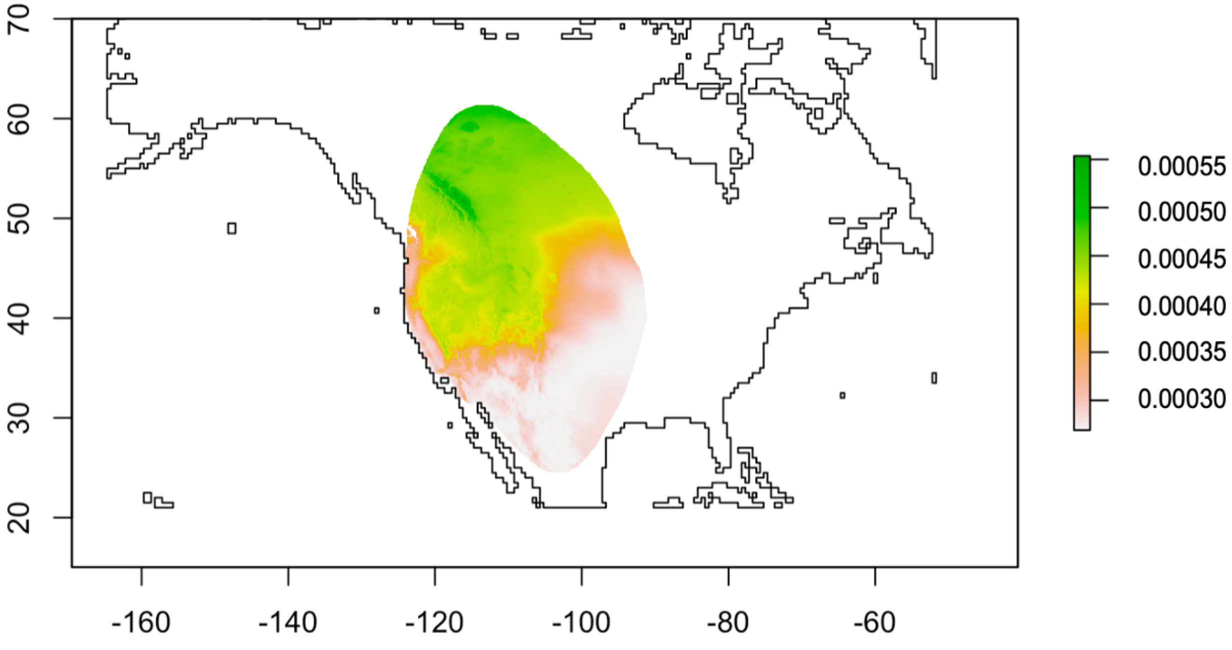


Figure 32: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the south central semiarid prairies in the fall of 2020 (*n* = 46).

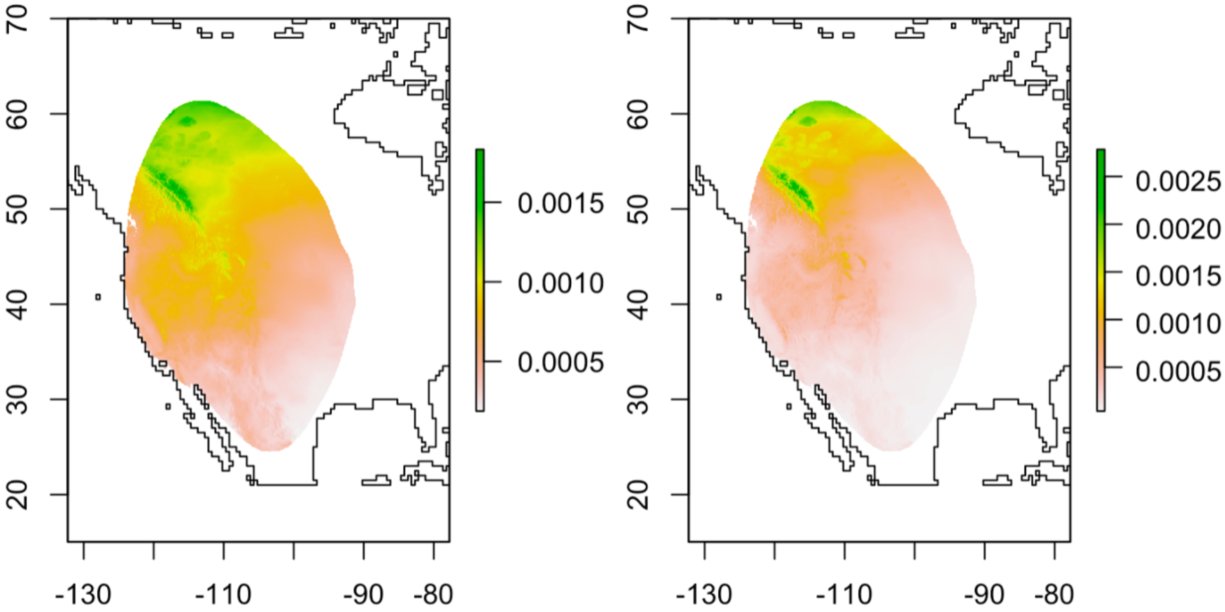


Figure 33: Union probability calculated for army cutworm moths (*Euxoa auxiliaris*) collected in the west-central semiarid prairies in the fall of 2020 (left; *n* = 85) and 2021 (right; *n* = 60).