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Using Stable Isotopes to Determine Natal Origin and Feeding Habits of the Army Cutworm Moth, *Euxoa auxiliaris* (Lepidoptera: Noctuidae)

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Abstract

The army cutworm, *Euxoa auxiliaris* (Grote), is a migratory noctuid that is both an agricultural pest and an important late-season food source for grizzly bears, *Ursus arctos horribilis* (Linnaeus, Carnivora: Ursidae), within the Greater Yellowstone Ecosystem. Beyond the confirmation of the moths' seasonal, elevational migration in the mid-1900s, little else has been documented about their migratory patterns. To address this missing ecological component, we examined (1) migratory routes during their spring and fall migratory periods throughout their natal range, the Great Plains, and (2) natal origin at two of their summering ranges 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, rather than migrating exclusively east to west, army cutworm moths are also migrating north to south during their spring migration. Moths did not exhibit natal origin site fidelity when returning to the Great Plains. Migrants collected from the Absaroka Range had the highest probability of natal origin in Alberta, British Columbia, Saskatchewan, the most southern region of the Northwest Territories, and second highest probability of origin in Montana, Wyoming, and Idaho. Migrants collected in the Lewis Range had the highest probability of origin in the same provinces of Canada. Results suggest that migrants of the Absaroka Range fed exclusively on C3 plants as larvae and rarely fed in heavily fertilized agroecosystems.

Key words: insect migration, Great Plains, Rocky Mountains, Noctuidae, deuterium

Migrating insects link geographically disparate landscapes through the exchange of energy, nutrients, pathogens, and biomass (Satterfield et al. 2020). Recent work has begun to illustrate the extent to which these movements may affect ecosystems on a global scale (Hu et al. 2016), and many insect migrants are key in agriculture; whether as pests or biological control agents (Showers et al. 1993, Wotton et al. 2019, Wu et al. 2021), as well as conservation (Brower et al. 2012, Flockhart et al. 2013, Chapman et al. 2015), and ecosystem function (Warrant et al. 2016). Despite the important ecological implications of these migrating insects, most research has centered on understanding vertebrate migration (Dingle 2014), and, for the

few species that have been studied, we often lack a comprehensive understanding of a population's flightpaths, such as where the population may overwinter (Chapman et al. 2015).

One such migratory insect, the army cutworm moth, *Euxoa auxiliaris* (Grote), straddles the intersection of agriculture and conservation. 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 (Strickland 1916, Seamans 1928, Walkden 1950, Burton et al. 1980). Pupation then occurs, and adults emerge in the late spring and early summer and migrate via flight west to high elevations in the Rocky Mountains, escaping the hot summer temperatures and dwindling resource availability of their natal range (Jacobson and Blakeley 1959, Pruess and Pruess 1967, Hardwick and Lefkovitch 1971).

This migration marks the export of potentially billions of calories from the Great Plains into the Rocky Mountains (Dittemore 2022). Upon reaching the Rocky Mountains, army cutworm moths feed on alpine flower nectar during the night and metabolize these calories into lipid reserves (Kendall 1981, Kevan and Kendall 1997). These lipid-dense organisms may constitute a significant portion of grizzly bear, *Ursus arctos horribilis* diets, as well as other vertebrates that occupy these talus-covered slopes (Mattson et al. 1991, French et al. 1994, Lozano 2022). Grizzly bears forage for these 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 Greater Yellowstone Ecosystem (Mattson et al. 1991, French et al. 1994, White et al. 1998a), and availability coincides with a period that is critical for bears to gain fat (Nelson et al. 1983, White 1996). Given the recent decline in other critical food sources of grizzly bears, such as cutthroat trout, whitebark pine seeds, and ungulates (for some areas) (Koel et al. 2005, Fortin et al. 2013, Schwartz et al. 2014, Manen et al. 2016), the army cutworm moth has likely become increasingly important. At the conclusion of the summer, surviving moths return to the Great Plains to mate, oviposit, and die (O'Brien and Lindzey 1994, Kevan and Kendall 1997, White et al. 1998b).

Despite the significance of this moth in both agriculture and the conservation of the grizzly bear, our understanding of the migratory ecology of the army cutworm moth is extremely limited. To date, only one study has attempted to provide a better understanding of its migratory patterns. Using three microsatellites (groups of repetitive, noncoding genes) in moths collected both at peaks of conservational interest and at lower elevations, Robison (2009) demonstrated that the moths were panmictic, i.e., moths mate randomly. 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 (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 in early hyperphagia 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 (Wassenaar and Hobson 1998). This technique has experienced 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 insights about the organism's biome (Wassenaar 2009, Quinby et al. 2020).

Stable hydrogen, or δ^2H, has been used in studies to track insect movement (Wassenaar and Hobson 1998; Brattström et al. 2010; Hobson et al. 2012, 2018, 2022; Flockhart et al. 2013, 2017; Yang et al. 2016). This isotope 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 origin (Hobson and Wassenaar 2019). This is especially true when applied to systems within North America because these patterns are highly pronounced along a north-south gradient (Bowen et al. 2005; West et al. 2006, 2009).

For insects, stable hydrogen tissue compositions (which are ultimately derived from and representative of the hydrosphere) are fixed into tissues as the insects develop and feed. Thus, metabolically inert, chitinous tissues (e.g., wings) are representative of larval feeding habits, and wings collected from adults can be analyzed and referenced against a map of predicted δ^2H values to determine natal origin of the sample (Wassenaar and Hobson 1998, Hobson et al. 2018). Stable hydrogen values of adult army cutworm moth wings should primarily be representative of larval feeding at natal origin sites, as the longest known larval migration to reach a new food source was limited to 3 miles (Wilcox 1898). If, however, larval feeding occurred on irrigated crops, adult δ^2H wing values would most likely be representative of surface water δ^2H values (Perdue and Hamer 2019), as opposed to precipitation-derived δ^2H values. Although surface water δ^2H values are largely driven by variation in precipitation δ^2H values, resulting δ^2H wing values would likely to be enriched compared to precipitation δ^2H values, ultimately increasing the amount of variance associated with δ^2H values for a specific area and reducing the amount of geographic specificity associated with this stable isotope (Bowen et al. 2007).

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

To better understand the army cutworm moth's migratory routes and larval feeding (and, in turn, how these inform grizzly bear management), our objectives were to:

(1) characterize the natal origin of army cutworm moths collected on mountain peaks of conservational interest within the Absaroka Range and the Lewis Range,
(2) determine whether army cutworm larvae 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, Lepidoptera: Noctuidae) wing δ^2H values (δ^2H_w), and environmental waters established by Hobson et al. (2018). We expected that moths collected within the Absaroka Range would have originated from

areas farther south when compared to the natal origin of moths collected within the Lewis Range. We hypothesized that most migrants collected in the Absaroka Range would have originated from a similar latitude, such as the Bighorn Basin or areas farther east. Similarly, we anticipated that moths migrating from and returning to the Great Plains would travel along latitudinal bands.

For moths collected within the Absaroka Range, we assessed the agricultural intensity of natal origin sites and determined whether larvae fed in C3 or C4 biomes using $\delta^{15}N$ measurements and $\delta^{13}C$ values, respectively. Although agricultural practices vary widely throughout the natal range of this moth, we expected to see most $\delta^{15}N$ wing values centering on 15‰ (indicating that moths had fed in agriculturally intensive areas). Finally, given the generalist feeding habits of army cutworm larvae, we expected that moths would have a mixture of carbon stable isotope composition similar to that of both C3 and C4 plants.

Materials and Methods

Study Area

Our study encompassed both 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 and Dietz 2020). Broadly, growing season 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 and Dietz 2020). Climate has been previously described in more detail in Rosenberg (1987) and Kunkel et al. (2013).

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 C4 crop dominated 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 (also C4) producers include Kansas and Texas (USDA 2022).

Of the army cutworm moth summering regions, our study included peaks within the Absaroka Range of northwestern Wyoming and the Lewis Range of northwestern Montana. Within the Absaroka Range, elevation ranges 1,830–4,006 m, wherein moth site elevations range 2,700–3,500 m (Mattson et al. 1991, French et al. 1994). The geology of moth sites is dominated by talus fields that lack vegetation and lie beneath the uppermost steep cliffs (Mattson et al. 1991, French et al. 1994, O'Brien and Lindzey 1994). Moth populations are supported by neighboring patches of lush vegetation and even larger meadows, supported by seasonal snowmelt and rain delivered from these cliffs. These plants flower, producing nectar that is critical for moths that forage locally to gather carbohydrates that are subsequently biosynthesized to lipids and accumulated for their return flights (French et al. 1994). Vegetation, climate, and geology have been described previously for the Absaroka Range (Baker 1944, Waddington and Wright 1974, Dirks and Martner 1982,

Thilenius and Smith 1985, Marston and Anderson 1991, Sundell 1993). Within the Lewis Range, elevation ranges 948–3,190 m, and its geology, vegetation, and climate have also been described previously (Willis 1902, Choate 1963, Finklin 1986, Damm 2001). Moth site elevations within the Lewis Range are similar to those found within the Absaroka Range, using grizzly bear presence as a proxy for army cutworm moth presence (White et al. 1998a).

Sample Collection: Great Plains

From 2018 to 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 contiguous ecoregions, including the west-central semiarid prairies, western cordillera, cold deserts, south-central semiarid prairies, and warm deserts (Fig. 1; Omernik and Griffith 2014). Collectors used either blacklight traps or collected army cutworm moths by hand and euthanized them by placing them in the freezer or by placing in sealed containers with insecticidal strips (e.g., Hot Shot No-Pest Strip Insect Killer Strips).

From 2020 to 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 as described above. Samples collected from 2018 to 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 × 8.89 cm (2.25″ × 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 potentially 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 named ecoregion are summarized in Tables 1 and 2.

Sample Collection: Moth Aggregation Sites (Mountain Peaks)

From 2017 to 2021, we hand-collected army cutworm moths from the talus at three moth aggregation sites in the Absaroka Range. Moths were immobilized on site by gently squeezing their thorax. All samples from 2017 to 2020 were stored in 6.35 × 8.89 cm (2.5″ × 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; these samples were shipped and stored as described previously. We cannot identify the specific peaks due to concerns regarding ecological disturbance in these sensitive areas (Nunlist 2020). 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 single moth samples from each peak and year to prepare for stable carbon and stable nitrogen analysis (or the total
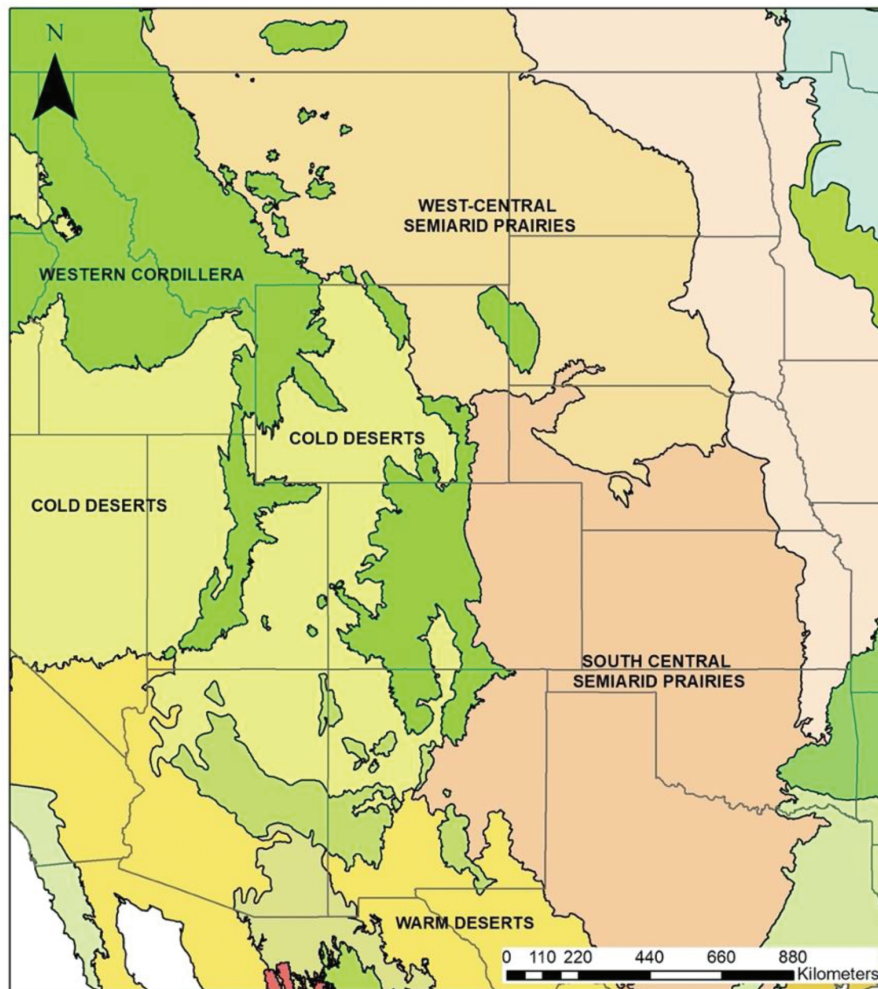
Fig. 1. The ecoregions used to delineate the groupings of spring and fall army cutworm moth, *Euxoa auxiliaris*, samples, including the west-central semiarid prairies, south central semiarid prairies, cold deserts, and western cordillera (EPA 2022). Only labeled ecoregions were used to group samples.

n for each peak and year if <50). Data from army cutworm moths collected at moth aggregation sites are summarized in Tables 3–6.

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 dissection to scrutinize genitalia for every sample; instead, we randomly selected five moths from each county/year or moth aggregation site/year combination.

Sample Preparation and Laboratory Analysis

All wing samples were placed into 20-ml glass 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 5 × 3.5-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 and Hobson 2000). Stable hydrogen values of the nonexchangeable portion of hydrogen were determined using comparative equilibration (Wassenaar and 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:

Table 1. Summary of δ²H$_w$ data for army cutworm moths, *Euxoa auxiliaris*, collected during the spring emergence period within the Great Plains (2018–2021, *n* = 1,031)

			δ2H (‰ VSMOW[a])	
Year	Ecoregion	*n*	Mean ± SD	95% CI
2018	Cold deserts	6	–150.7 ± 25.2	–177.2 to –124.3
2019	Cold deserts	108	–127.9 ± 21.3	–131.9 to –123.8
2020	Cold deserts	161	–132.1 ± 22.3	–135.6 to –128.7
2021	Cold deserts	33	–122.8 ± 27.4	–132.6 to –112.9
2018	Western cordillera	4	–166.3 ± 2.0	–169.5 to –163.1
2019	Western cordillera	18	–142.6 ± 23.6	–154.3 to –130.9
2020	Western cordillera	62	–145.1 ± 20.5	–150.3 to 139.9
2021	Western cordillera	16	–159.2 ± 14.8	–167.1 to –151.3
2018	SC semiarid prairies[b]	45	–118.7 ± 15.7	–123.5 to –114.0
2019	SC semiarid prairies	67	–116.5 ± 19.9	–121.4 to –111.7
2020	SC semiarid prairies	177	–119.1 ± 12.3	–120.9 to –117.3
2021	SC semiarid prairies	103	–130.8 ± 13.0	–120.9 to –117.3
2020	Warm deserts	22	–130.6 ± 10.5	–133.4 to –128.3
2020	WC semiarid prairies[c]	189	–130.8 ± 12.3	–132.6 to –129.0
2021	WC semiarid prairies	20	–159.5 ± 19.8	–168.8 to –150.2

[a]Vienna Mean Standard Oceanic Water.
[b]South central semiarid prairies.
[c]Western central semiarid prairies.

Table 2. Summary of δ²H$_w$ for army cutworm moths collected during the fall migratory period within the Great Plains (2020–2021, *n* = 293)

			δ2H (‰ VSMOW[a])	
Year	Ecoregion	*n*	Mean ± SD	95% CI
2020	Cold deserts	38	–122.4 ± 13.9	–127.0 to –117.8
2020	Western cordillera	49	–133.9 ± 19.4	–139.5 to –128.3
2021	Western cordillera	14	–154.9 ± 25.9	–169.8 to –139.9
2020	SC semiarid prairies	46	–124.6 ± 20.6	–130.7 to –118.5
2020	WC semiarid prairies[+]	85	–132.3 ± 19.6	–136.5 to –128.0
2021	WC semiarid prairies	61	–145.3 ± 19.7	–150.4 to –140.2

[a]Vienna Mean Standard Oceanic Water.
[b]Western central semiarid prairies.

Table 3. Summary of δ²H$_w$ data for army cutworm moths collected each summer at mountain peaks within the Absaroka Range (2017–2021, *n* = 618)

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

[**]Vienna Mean Standard Oceanic Water.

Table 4. Summary of δ²H$_w$ data for army cutworm moths collected during the summer of 2019 within the Lewis Range (2019, *n* = 77)

			δ2H (‰ VSMOW[a])	
Year	Location	*n*	Mean ± SD	95% CI
2019	D	30	-145.5 ± 25.6	-155.0 to -135.9
2019	E	13	-197.0 ± 43.1	-223.0 to -171.0
2019	F	13	-178.8 ± 36.2	-200.7 to -156.9
2019	G	2	-158.9 ± 18.2	NA
2019	H	3	-170.9 ± 11.9	-200.5 to -141.4
2019	I	2	-179.3 ± 0.4	NA
2019	J	14	-174.0 ± 33.1	-193.1 to -154.9

[a]Vienna Mean Standard Oceanic Water.

Table 5. Summary of δ¹³C$_w$ data for army cutworm moths collected each summer at mountain peaks within the Absaroka Range (2017–2021, *n* = 205)

			δ ¹³C (‰ VPDB[a])	
Year	Location	*n*	Mean ± SD	95% CI
2020	B	6	–27.0 ± 0.8	–27.9 to –26.1
2021	B	33	–26.7 ± 2.3	–27.5 to –25.9
2017	A	29	–27.6 ± 1.4	–28.2 to –27.1
2018	A	29	–26.7 ± 1.2	–27.2 to –26.3
2020	A	25	–27.3 ± 1.3	–27.8 to –26.8
2019	C	17	–27.0 ± 3.7	–27.5 to –23.7
2020	C	23	–27.0 ± 1.0	–27.4 to –26.6
2021	C	43	–27.2 ± 1.0	–27.5 to –26.9

[a]Vienna Peedee Belemnite.

Table 6. Summary of δ¹⁵N$_w$ data for army cutworm moths collected each summer at mountain peaks within the Absaroka Range (2017–2021, *n* = 205)

			δ ¹⁵N (‰ VPDB[a])	
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

[a]Vienna Peedee Belemnite.

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

where R_{sample} and $R_{standard}$ are the $^2H/^1H$ of the sample and standard, respectively. Precision for δ²H 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 $\delta^{15}N$ and $\delta^{13}C$. Analyses were normalized to the laboratory standards. Laboratory standards were calibrated against IAEA N1, IAEA N2, and USGS 43 for $\delta^{15}N$ and NBS 21, NBS 22, and USGS 24 for $\delta^{13}C$. The three internal laboratory standards used were: UNM-CSI Protein std#1, casein purchased from Sigma Aldrich with $\delta^{15}N$ and $\delta^{13}C$ values of 6.43 and –26.52‰; UNM-CSI Protein std#2, soy protein purchased from Sigma Aldrich with $\delta^{15}N$ and $\delta^{13}C$ values of 0.98 and –25.78‰; and UNM-CSI protein Std#4, house made tuna protein with $\delta^{15}N$ and $\delta^{13}C$ values of 13.32 and –16.17‰.

Statistical Analysis

All statistical analyses were performed in R version 4.0.2 (Team 2020). We fit linear models using base R and assessed the models for assumption violations using the *plot* function. The *Anova* and *anova* functions from the 'car' package were used to perform two-way and one-way ANOVA, respectively (Fox and Weisberg 2019), and we performed Tukey's Honest Significant Difference using the *glht* function from the 'multcomp' package (Hothorn et al. 2008). The two-sample t-test was performed using the *t.test* function from base R and assessed normality by generating a histogram with the *ggplot* function from the 'ggplot2' package (Wickham 2016). The *ggplot* function was also used to create boxplots. To generate a tissue-specific wing isoscape, re-calibrate our sample values according to the stable isotope standards used by Hobson et al. (2018), compute the posterior probability of sample origin, aggregate probabilities from all samples, and create maps of natal origin, we used functions from the 'assignR' package (Ma et al. 2020), as will be discussed in further detail below. All plots used to assess assumptions accompanying statistical tests are listed in Appendix S1 (Supp Figs. 1–6 [online only]).

Spring and Fall Samples

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 and 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 found between ecoregions and established that there was very strong evidence for a difference in mean δ^2H_w between ecoregions. We performed a post-hoc analysis with Tukey's Honest Significant Difference (HSD, α= 0.05).

Moth Aggregation Site Samples

We extracted the Bighorn Basin's predicted δ^2H_w value with a 1-degree buffer from the wing tissue-calibrated isoscape (Hobson et al. 2018). 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. Strong evidence for 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 little to no evidence for 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). Given that both *E. auxiliaris* and *M. unipuncta* belong to the Noctuidae family, we assumed that these moths have the same differentiation factor when integrating stable hydrogen into their tissues. 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 $\delta^2 H_w$ (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 $\delta^2 H_w$ 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 (Fig. 2). Exceptions to this finding (wherein there was strong evidence or differences in stable hydrogen distributions as compared to other years of collection within the ecoregion) included 2021/south-central semiarid prairies and 2020/west-central semiarid prairies. There was very strong evidence that most geographically distinct ecoregions—the western cordillera and south-central semiarid prairies—were different for all year combinations excluding western cordillera/2019 and south-central semiarid prairies/2021 (Fig. 2).

Fall Samples
Although there was strong evidence that both year and ecoregion had an effect on mean $\delta^2 H_w$ (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 $\delta^2 H_w$ (ANOVA, $F_{1,286} = 1.4$, $p = 0.24$). Using the additive model ($\delta^2 H_w$ as a function of year + ecoregion), we found very strong evidence for a difference in mean $\delta^2 H_w$ values 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 $\delta^2 H_w$ values were less distinctive than those found in the spring, more northern ecoregions tended to have more negative distributions (Fig. 3).

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 (Appendix S2: Supp Fig. 1 [online only]). 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 potential range across all years, 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 (Supp Figs. 4 and 6 [online only]). 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 (Appendix S2: Supp Figs. 3 and 5 [online only]).

Moth Aggregation Site Samples
We found very strong evidence for a difference in mean $\delta^2 H_w$ 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. 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 $\delta^2 H_w$ 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 $\delta^2 H_w$ from moths collected within this region was comparable to the Bighorn Basin 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; Fig. 4), and there was very strong evidence that mean $\delta^2 H_w$ 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 $\delta^2 H_p$ 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 $\delta^2 H_w$ values from all peaks. Moths of this range had a 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 (Appendix S2: Supp Fig. 2 [online only]). 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 (Fig. 4). 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
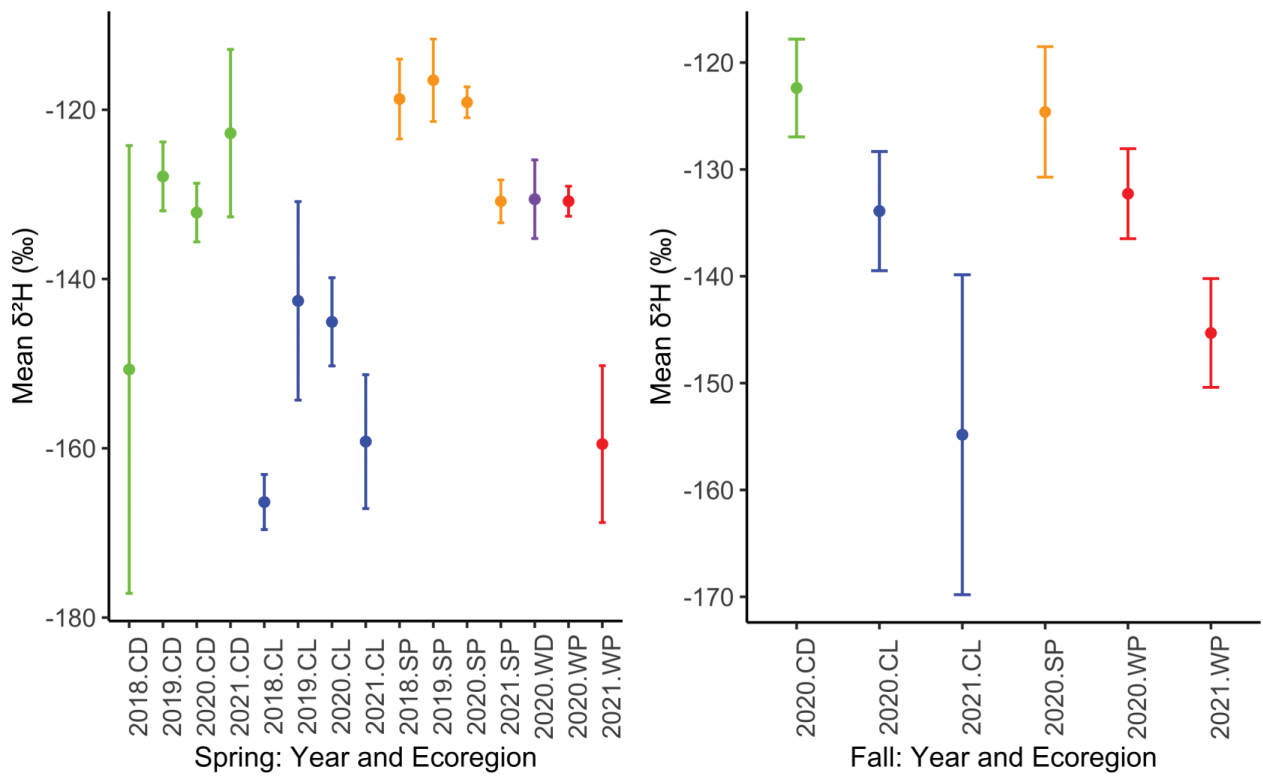
Fig. 2. Stable hydrogen means (dots) and the associated 95% confidence interval (whiskers) of army cutworm moths, *Euxoa auxiliaris,* grouped per ecoregion and year of collection (2018–2021). Spring collection is included in the left panel, and fall collection is included in the right panel. Labels of the x-axis denote the year and ecoregion (YYYY.Ecoregion), wherein 'CD' indicates the cold deserts, 'CL' indicates the western cordillera, 'SP' indicates south-central semiarid prairies; 'WD' indicates the warm deserts, and 'WP' indicates west-central semiarid prairies. See Table 1 for sample sizes.
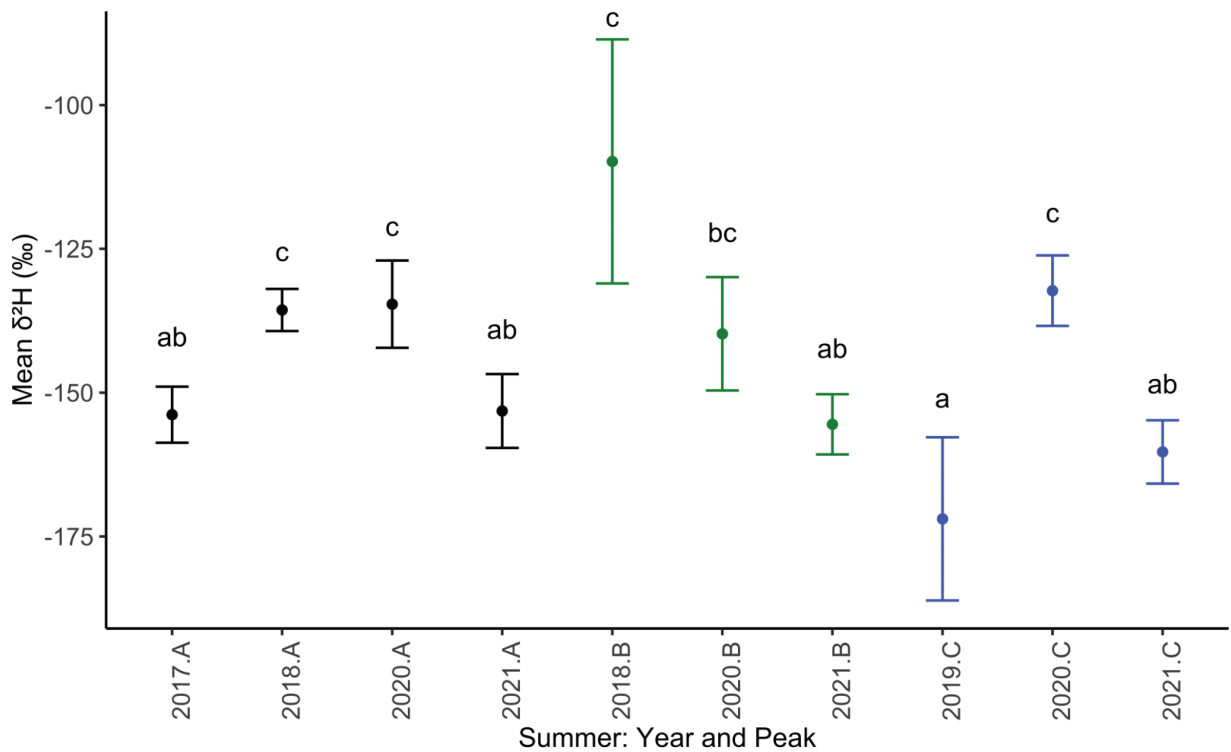
Fig. 3. Stable hydrogen means (dots) and the associated 95% confidence interval (whiskers) of army cutworm moths, Euxoa auxiliaris, collected within the Absaroka Range during the summer, grouped according to both the peak and year of collection—'YYYY.Peak' (2017–2021). A line with no letter in common 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.

characterized by very diverse origins in addition to patterns found in all years. Moths collected in 2017 had a moderate probability of origin in parts of Washington, Oregon, California, Nevada, Utah, and Colorado (Fig. 4a). In 2020, migrants may have originated from any state within their natal range (Fig. 4d). The probable origin of migrants collected in both 2019 and 2021 were again constrained primarily to the northwestern extent of their range (Figs. 4c and e).

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 $\delta^{13}C_w$ value close to, if not exactly, –27‰ (Table 5). Although there was limited evidence that $\delta^{13}C_w$ values varied between peaks (ANOVA, $F_{2,197} = 0.87$, $p = 0.42$), there was strong evidence for 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.

Nitrogen stable isotope composition, however, did not vary substantially 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 $\delta^{15}N$ 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 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. We found very strong evidence for differences in mean δ^2H_w 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. Although previous studies observed flights of army cutworm moths orienting southwest (Pepper 1932, Hendricks 1998), this study is the first to provide evidence for north to south movement. 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. There was very strong evidence that mean δ^2H_w of the Lewis Range was different 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 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). Our findings corroborate Robison's (2009) discovery that army cutworm moths are panmictic and, conversely, provide little support for the hypothesis that migrants were primarily supplied by the Bighorn Basin (O'Brien and Lindzey 1994).

Carbon stable isotope composition of moths collected in the Absaroka Range was 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 surprising, as most migrants likely originated from regions dominated by cool-season grasses and cropland. Furthermore, corn and sorghum (cultivated C4 plants) are planted in the late spring, and germination may occur after the window of adult moth emergence for some areas (Carter et al. 1989, Kucharik 2006). However, this may also 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. Surprisingly, of the individuals that fed on C4 plants, only one migrant clearly originated from an agroecosystem that was heavily fertilized.

Across summer, spring, and fall collection, there was strong evidence that year had an effect on both moth δ^2H_w and $\delta^{13}C_w$. This finding 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 sporadic status of army cutworm moths 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 north of 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 1,800 km. Comparatively, both the Australian Bogong moth, *Agrotis infusa* (Boisduval, Lepidoptera: Noctuidae), and black cutworm, *Agrotis ipsilon* (Hufnagel, Lepidoptera: Noctuidae), undertake a bi-annual migration of as far as 1000 km and weather-assisted migration of as far as 1,266 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 and Pruess 1964). Thus, to complete such a migration in the time frame between adult emergence in Canada and the
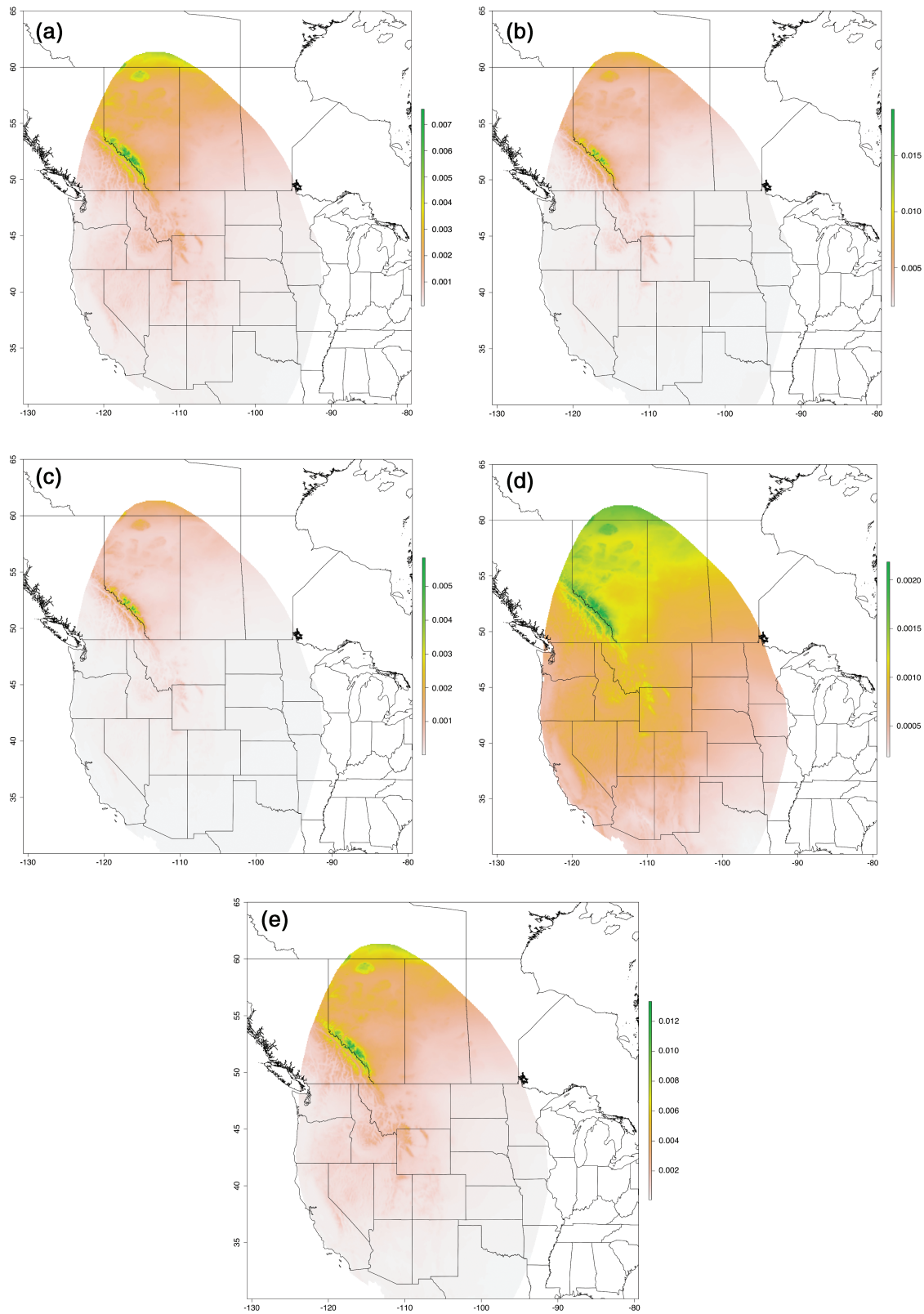
Fig. 4. Union probability, the probability that any army cutworm moth (*Euxoa auxiliaris*) from the group originated from any cell within the army cutworm moth's known range, calculated for the Absaroka Range (panel a: 2017, *n* = 79; panel b: 2018, *n* = 278; panel c: 2019, *n* = 20; panel d: 2020; *n* = 87; panel e: 2021; *n* = 150). 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).

onset of summer in the Rocky Mountains (slightly less than a month), army cutworm moths would likely need to fly using the aid of preferential winds that occur either within or above the insect flight boundary layer, of which the latter is seen in the aforementioned noctuid migrants (Showers et al. 1989a; Chapman et al. 2008a,b).

As we mentioned previously, the conclusions are limited using an isoscape based on a stable isotope that varies primarily along a north-south gradient. The resolution and accuracy of the assignments we presented here would be greatly improved with the inclusion of a second isotope, such as sulfur, and potentially a trace element (Holder et al. 2014, Heinrich and Collins 2017). 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. That is, 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. It is possible that stable hydrogen values were more negative than predicted in some areas of Canada (Jasechko et al. 2017), or army cutworm moths integrate stable hydrogen values into their tissues in a way that discriminates against deuterium. Given that both *E. auxiliaris* and *M. unipuncta* belong to the family Noctuidae, it is unlikely that significant differences would be found between the metabolic pathways of these two insects. As such, both *E. auxiliaris* and *M. unipuncta* likely integrate stable isotopes into their tissues with a similar fractionation factor. Verification 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 via captive rearing, would be of substantial use in rectifying this limitation.

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 geographically diverse array of natal origin sites and provide the first evidence that army cutworm moths may migrate northwest to southeast, in addition to previously documented east to west movement.

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Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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