

Seasonal occurrence, body composition, and migration potential of army cutworm moths in northwest Montana

Don White, Jr., Katherine C. Kendall, and Harold D. Picton

Abstract: Grizzly bears (*Ursus arctos horribilis*) consume adult army cutworm moths (*Euxoa auxiliaris*) from late June through mid-September on alpine talus slopes in Glacier National Park (GNP), Montana. As part of a study carried out to better understand the ecological interactions between grizzly bears and army cutworm moths in GNP, we studied temporal abundance patterns, body mass and composition, and migration potential of moths collected from alpine moth aggregation sites throughout the summer of 1994 and 1995. Army cutworm moths arrived in the alpine zone of GNP in late June or early July and departed by late August or early September. While moths were in the alpine zone, their body mass and moisture, lipid, and gross energy contents markedly increased and crude protein decreased. The absence of moths from the alpine zone coincided with the presence of moths on the Great Plains. Using published estimates of the cost of transport in flying animals, we calculated that an army cutworm moth flying in late summer through still air could fly 140 km using body lipid reserves alone.

Résumé : Les Grizzlis (*Ursus arctos horribilis*) consomment des Légionnaires grises (*Euxoa auxiliaris*) de la fin de juin à la mi-septembre sur les pentes du talus alpin du parc national Glacier au Montana. Dans le cadre d'une étude conçue pour jeter de la lumière sur les interactions écologiques entre les Grizzlis et les légionnaires du parc Glacier, nous avons suivi les fluctuations de l'abondance, de la masse et de la composition corporelle, de même que le potentiel migratoire des légionnaires récoltées à leurs sites de rassemblement dans la zone alpine au cours des étés de 1994 et 1995. Les légionnaires sont arrivées dans la zone alpine du parc à la fin de juin et au début de juillet et en sont reparties à la fin d'août et au début de septembre. Au cours du séjour en zone alpine, la masse corporelle, le contenu en eau, le contenu en lipides et le contenu énergétique brut des légionnaires ont augmenté fortement et leur contenu en protéines brutes a diminué. L'absence des légionnaires dans la zone alpine coïncidait avec leur présence dans les Plaines. D'après les estimations publiées du coût de transport d'un animal au vol, nous avons calculé qu'une légionnaire se déplaçant au vol par temps mort à la fin de l'été pourrait parcourir 140 km sur ses seules réserves lipidiques.

[Traduit par la Rédaction]

Introduction

Army cutworm moths lay their eggs in the soil of the Great Plains in autumn and develop to the first or second larval instar before hibernation (Johnson 1905; Cooley 1916; Strickland 1916; Burton et al. 1980; Kendall 1981). In spring, the larvae begin feeding on a variety of plants such as alfalfa and small grains (Burton et al. 1980; Morrill 1991). After a total of 6 or 7 instars from egg to last molt, pupation occurs in underground cells (Snow 1925; Seamans 1927; Burton et al. 1980). In late May or early June the newly emerged adult moths enter a migratory phase and fly west into the Rocky Mountains, presumably to avoid the high temperatures of summer at lower elevations (Pepper 1932; Walkden 1950;

Chapman et al. 1955; Pruess 1967; Hardwick and Lefkovitch 1971; Burton et al. 1980). Army cutworm moths inhabit the interstices of alpine talus slopes diurnally throughout the summer in the northern Rocky Mountains (Mattson et al. 1991; French et al. 1994; O'Brien and Lindzey 1994; White et al. 1998).

Army cutworm moths do not mate until late summer or early autumn, when they return to the Plains. On the Plains the females enter a settling phase and oviposit 1000–3000 eggs per individual into the soil (Walkden 1950; Burton et al. 1980). The army cutworm moth is univoltine (Cooley 1916; Seamans 1927; Burton et al. 1980; Kendall 1981), and after oviposition the adult moths die.

Grizzly bears feeding on army cutworm moth aggregations excavated from alpine talus slopes have been documented in several areas in the northern Rocky Mountains (Chapman 1954; Chapman et al. 1955; Sumner and Craighead 1973; Craighead et al. 1982; Servheen 1983; Klaver et al. 1986; Aune and Kasworm 1989; Mattson et al. 1991; French et al. 1994; O'Brien and Lindzey 1994). Army cutworm moths are an abundant and important ephemeral food source for some grizzly bear populations in some years (Klaver et al. 1986; Mattson et al. 1991; O'Brien and Lindzey 1994; White et al. 1998). Presumably, moth foraging is physiologically feasible because army cutworm moths occupy talus slopes in large

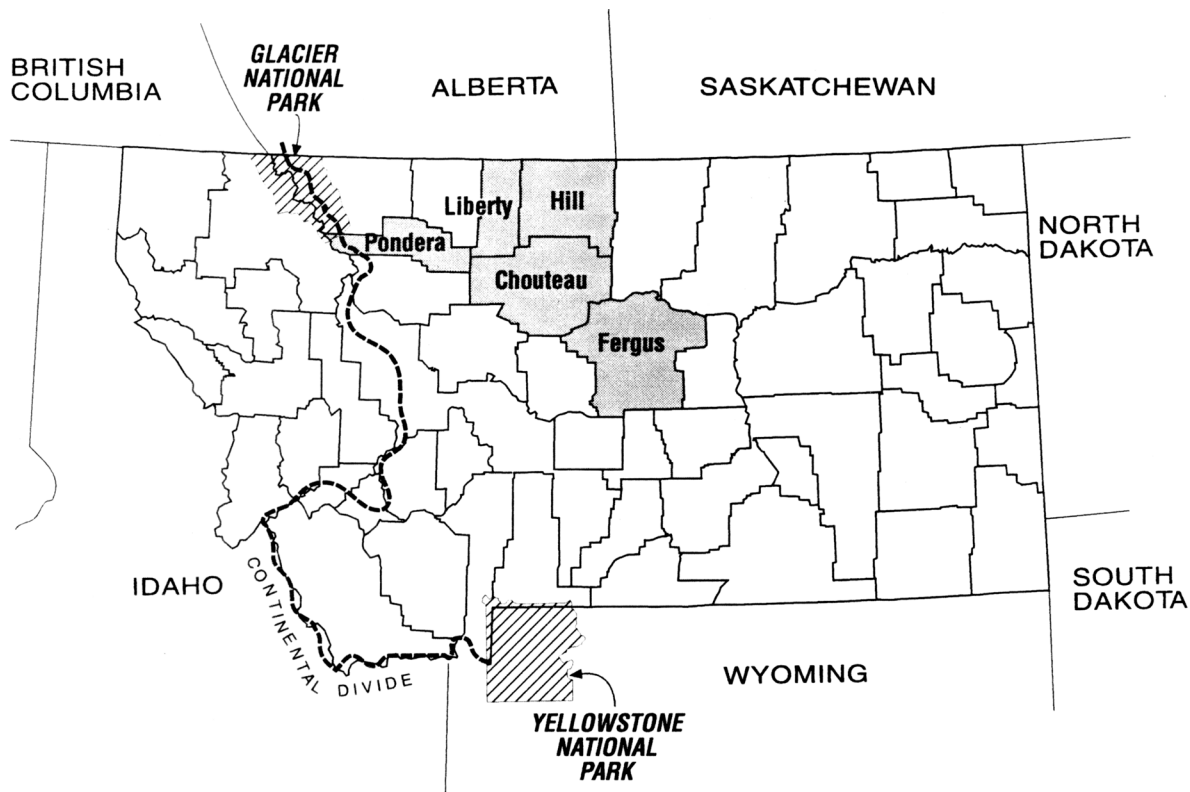
Received September 4, 1997. Accepted December 18, 1997.

D. White, Jr. Montana Tech of the University of Montana, Department of Biological Sciences, Butte, MT 59717-8997, U.S.A. (e-mail: dwhite@po1.mtech.edu).

K.C. Kendall. Biological Resources Division, U.S. Geological Survey (USGS), c/o Glacier National Park, MT 59937-0128, U.S.A. (e-mail: katherine_kendall@nbs.gov).

H.D. Picton. Montana State University, Bozeman, and Department of Fish and Wildlife Management and Research, Bozeman, MT 59717-0001, U.S.A. (e-mail: ubihp@ocsc.montana.edu).

Fig. 1. Map of Montana with the locations of counties where army cutworm moths were collected in late summer and early autumn, 1992–1995.



aggregations and, hence, consume a concentrated food supply. Moth densities varied severalfold among the talus sites we examined (D. White, Jr., K.C. Kendall, and H.D. Picton, in preparation). The density of moths on and within talus debris was $14.3/\text{m}^2$ of surface area ($\text{SD} = 17.2$, $n = 16$) in 1992, $6.7/\text{m}^2$ of surface area ($\text{SD} = 11.2$, $n = 16$) in 1994, and $5.8/\text{m}^2$ of surface area ($\text{SD} = 6.3$, $n = 16$) in 1995. Five areas selected for their especially high densities in 1992 had 111, 120, 132, 164, and 178 moths/ m^2 . We consider these estimates conservative; while digging into the talus to count moths, many escaped our detection by crawling out of the area being censused.

In years when cutworm moths are abundant, a grizzly bear can consume almost 40 000 per day, or about 2500 per hour (D. White, Jr., K.C. Kendall, and H.D. Picton in preparation). To better understand the nutritional and energy implications of such a concentrated food source, we tested the null hypothesis that there was no relationship between season and body composition of army cutworm moths taken from alpine sites. The hypothesis was tested by regressing total body moisture, crude protein, total lipid, and gross energy on season. A significant regression would lead to rejection of the null hypothesis. The timing of the autumn migration was studied by comparing moth departure from alpine study sites in Glacier National Park (GNP) with presence at traps located in 5 counties in Montana located approximately 150–200 km east and southeast of GNP. We then compared the body composition of moths from GNP with that of moths captured on the Plains. To learn more about moth abundance patterns, we also esti-

mated potential moth migration distances based upon late-summer whole-body lipid reserves. Finally, we considered the question of why army cutworm moths occupy alpine talus slopes during summer.

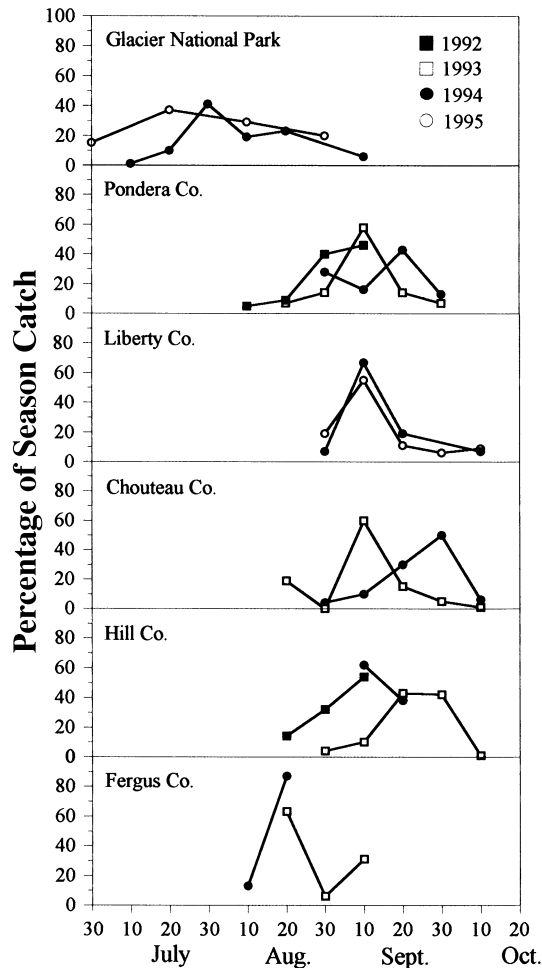
Study areas

GNP is located in northwestern Montana adjacent to British Columbia and Alberta (Fig. 1). Approximately one-third of GNP's 4100 km^2 occurs above timberline. Much of the remainder is forested with scattered meadows, which occur most frequently on the eastern side of the park. Relief is precipitous. Deep glaciated valleys and basins divide large, rugged mountain massifs. Many valleys are 1800 m below their surrounding summits (Carrara and McGimsey 1981). Elevations in the park range from 950 m at the Middle Fork – North Fork Flathead River confluence to 3190 m atop Mount Cleveland (Finklin 1986).

The climate of GNP is Continental with Pacific Maritime modifications, particularly on the western side of the park (Dightman 1967; Carrara and McGimsey 1981). The alpine climate is characterized by frequent strong (>66 km/h) winds, typically westerly in winter (December–February) and southwesterly during summer (July–August) (Finklin 1986). Precipitation generally increases with elevation, but decreases rapidly with horizontal distance east of the Continental Divide (Finklin 1986). Mean July temperatures range from 15 to 17°C in the lower valleys (Finklin 1986). Summer afternoon temperatures usually decrease with increasing elevation, at an average lapse rate of 7.5–8°C per 1000 m (Finklin 1986).

Our Plains study sites were wheat fields in Pondera, Liberty, Chouteau, Hill, and Fergus counties located in north-central Montana (Fig. 1). The climate of this region is characterized by frequent strong (>50 km/h) winds, northwesterly in winter and southwesterly during

Fig. 2. Seasonal occurrence of army cutworm moths at a light trap (elevation 2150 m in Glacier National Park) or pheromone traps (Pondera, Liberty, Chouteau, Hill, and Fergus counties) in Montana during summer and autumn, 1992–1995. Graphs are arranged approximately west to east (top to bottom).



summer. Most of the annual precipitation occurs in June (Caprio et al. 1997). Mean July temperatures range from 19 to 21°C (Caprio et al. 1997).

Methods

Moth-capture techniques

We used two methods to collect moths. A standard black-light trap using a 15-W Sylvania F8T5/BL fluorescent tube was the primary method used in the alpine zone to capture moths from late June through early September in 1994 and 1995. Each black light was powered by a 12-V DC marine battery. The number of moths captured per trap-night was used as an index of moth abundance in alpine moth aggregation sites throughout the summer. The killing agent was 10% formaldehyde and detergent. Traps were equipped with automatic light switches. As the traps were remotely located, requiring a 6-h hike one way, we emptied the traps and exchanged batteries approximately every 7 days in 1994 and 14 days in 1995.

To compare body composition of moths captured at alpine moth aggregation sites in GNP with that of moths captured on the Plains and to determine the timing of the autumn migration, sex-attractant traps (Unitrap, Phero Tech. Inc., Vancouver, British Columbia) baited with army cutworm lure (Terochem Laboratories Ltd., Edmonton, Alberta) were used. Prior to placement in the field, each trap was

positioned near the top of a wooden stake (approximately 200 × 4 × 1 cm) and tied securely with plastic baling twine. At each trap site, 2 traps spaced 10 m apart were placed adjacent to a wheat field. Locations with high road grade, deep ditches, or any other feature that might alter the air-flow pattern were avoided. At the trap site, the stake with the attached trap was driven into the ground so that the trap was 1.5 m above ground level. Traps were checked weekly and captured moths were removed, counted, and frozen in plastic bags. Trap construction, placement, and monitoring were conducted by Montana State University—Bozeman Agriculture Extension Agents. Light traps were used at each of our Plains study sites in July and August in 1994 and 1995 to confirm the absence of adult army cutworm moths.

Body composition of moths

To assess nutritional value and potential moth migration distances, we investigated moth body composition. Gross energy and crude protein of collected moths were determined by bomb calorimetry (1 cal = 4.1868 J) and macro-Kjeldahl ($N \times 6.38$), respectively. Lipid content was determined using a Soxhlet apparatus and total moisture content was determined via mass difference before and after drying. Except for total moisture content, body composition analyses are reported on a dry mass basis. Moths were stored frozen (0°C) in dry, sealed containers to minimize dehydration prior to analysis. Body composition did not differ between males and females, therefore samples were combined for analyses. At least 20 moths were used for each analysis for each sampling period. All samples were measured in duplicate and the means are reported. All analyses were conducted at the Analytical Laboratory, Montana State University—Bozeman. Seasonal changes in body composition of moths were analyzed using least-squares linear regression. We accepted ≤ 0.05 as significant.

Results

Chronology of moth migrations

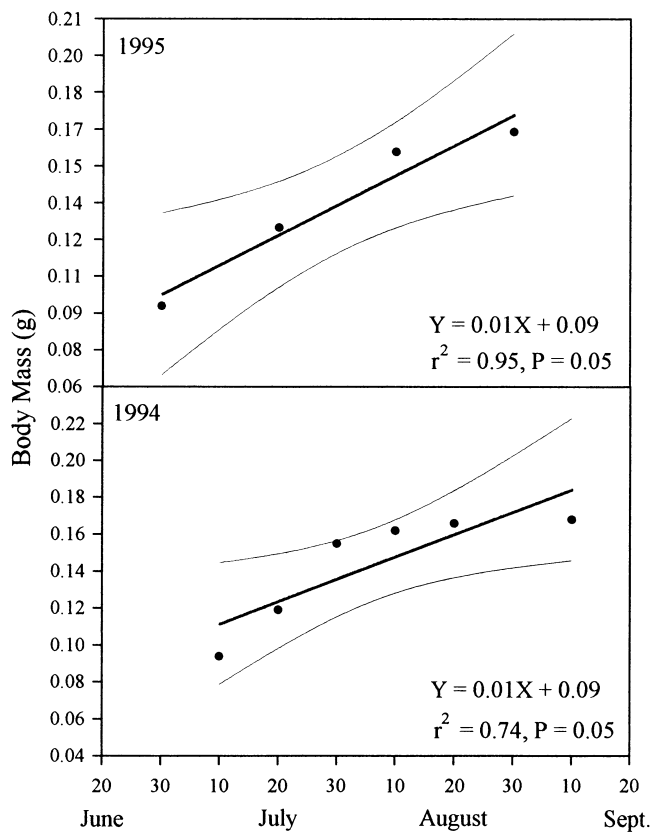
Army cutworm moths arrived in the alpine zone of GNP approximately 2 weeks later in 1994 than in 1995: early July in 1994 and late June in 1995 (Fig. 2). Moth abundance peaked in late July in 1994 and mid-July in 1995. We did not capture any army cutworm moths after 10 September in 1994 or after 30 August in 1995 (Fig. 2). The earliest we captured moths on the Plains was early August and none were captured after 10 October. The absence of moths from the alpine zone coincided with presence of moths on the Plains (Fig. 2).

Body composition of moths

Army cutworm moth body mass and total moisture, total lipid, and gross energy contents increased markedly while the moths were in the mountains and decreased as they migrated back to the Plains in the autumn. Upon arrival in the alpine zone of GNP, moths each weighed approximately 0.10 g. When the moths left the alpine in late summer, they each weighed approximately 0.17 g, a 70% increase in body mass in 8 weeks (Fig. 3). There was a corresponding increase in total body moisture content (Fig. 4). Total lipid content was 40–55% between late June and mid-July and rose to about 65% by the end of the summer (Fig. 5). Gross energy content of moths increased from approximately 6 kcal/g in late June or early July to almost 8 kcal/g in early September in 1994 and 1995 (Fig. 6). In contrast, while levels of crude protein remained stable, its proportion of dry mass declined from 35–40% in June to 25% in early September (Fig. 7).

The nutritional content of moths collected in late summer or early autumn on the Plains declined sharply from levels in

Fig. 3. Body masses of army cutworm moths captured at a light trap (elevation 2150 m) located adjacent to an alpine moth aggregation site in Glacier National Park, Montana, 1994–1995. The curved lines denote the 95% confidence interval of the regression line.



alpine collections. Total lipid content decreased from a high of about 70% in the alpine zone to 9–28% in Pondera and Liberty counties. Concurrent with low lipid levels, gross energy content of moths on the Plains ranged from 3 to 6 kcal/g compared with 8 kcal/gm in the mountains (Table 1).

Total moisture content of moths captured on the Plains varied widely, from 6% in Liberty County in 1994 to 65% in Pondera County in 1995. Total lipid content of moths captured on the Plains was higher in 1994 than in 1995 (Table 1).

Migration potential

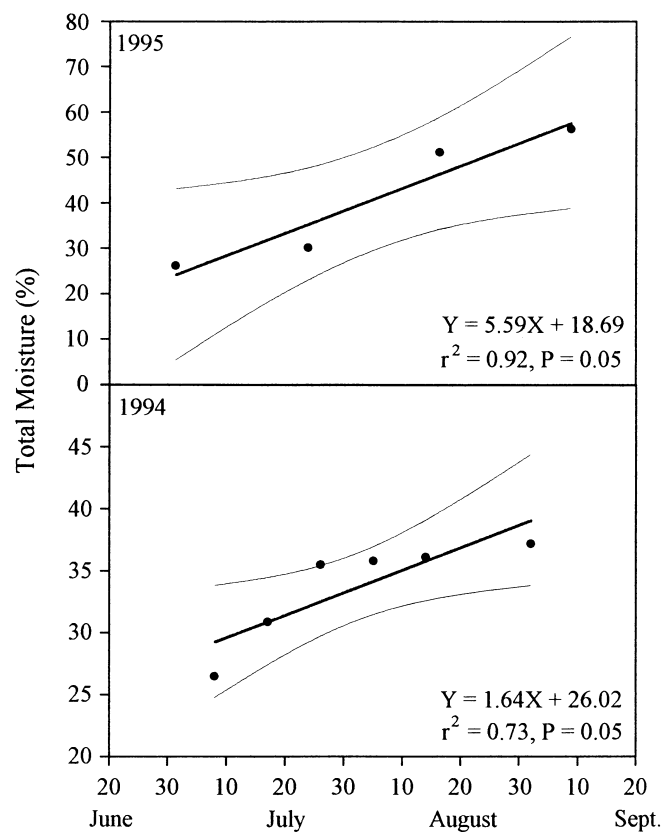
If a 0.17-g moth (0.085 g dry matter) uses fat equivalent to 60% of its initial dry-matter body mass during migration, the total energy yield is 0.474 kcal (0.06 g of lipid catabolized, 9.3 kcal/g of lipid). From Schmidt-Nielsen's (1972) analysis of the cost of transport for flying animals, the cost of transport for a 0.17-g moth is approximately $0.020 \text{ kcal/g/km} \times 0.17 \text{ g} = 0.0034 \text{ kcal/km}$. Thus, a moth flying through still air, presumably at a speed that minimizes the cost of transport, metabolizing lipid reserves alone, could travel $0.474 \text{ kcal} / 0.0034 \text{ kcal/km} = 140 \text{ km}$.

Discussion

Chronology of moth migrations

Spring flights of army cutworm moths occur as early as April

Fig. 4. Total body moisture content of army cutworm moths captured at a light trap (elevation 2150 m) located adjacent to an alpine moth aggregation site in Glacier National Park, Montana, 1994–1995. The curved lines denote the 95% confidence interval of the regression line.

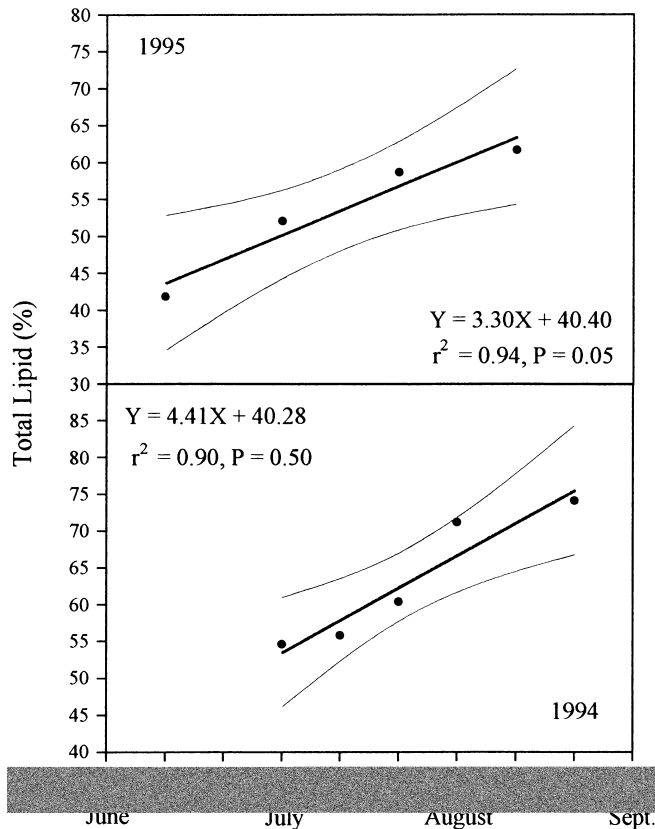


in Arizona, May and June in Nebraska, and July in Canada (Pruess 1967). Using black-light traps in Nebraska and Wyoming from 1959 to 1965, Pruess (1967) demonstrated that spring flight activity was predominantly from east to west. Autumn flights, however, have not received as much study as spring flights. In light traps, Pruess (1967) began capturing army cutworms in mid to late August in Wyoming and late August and early September in Nebraska. The appearance of army cutworms in our sex-attractant traps in 5 counties of north-central Montana in mid to late August, coinciding with the disappearance of moths from alpine regions of GNP, supports the migration hypothesis proposed by Pruess (1967).

Body composition of moths

Total lipid and gross energy contents of army cutworm moths increased linearly during their summer visit to GNP. Similarly, army cutworm moths showed an overall increase in abdominal lipid content over the summer months on Pennsylvania Mountain, Colo. (Kendall 1981). Mean abdominal lipid content in June for army cutworm moths captured in 1979 and 1980 was 38 and 46%, respectively. Mean abdominal lipid content in July for moths captured in 1978–1980 was 72, 51, and 64%, respectively (Kendall 1981). O'Brien and Lindzey (1994) also found a seasonal increase in whole-body lipid content in army cutworm moths captured near alpine moth aggregation sites in the Absaroka Mountains, Wyo.

Fig. 5. Total lipid content (ether extract) of army cutworm moths captured at a light trap (elevation 2150 m) located adjacent to an alpine moth aggregation site in Glacier National Park, Montana, 1994–1995. The curved lines denote the 95% confidence interval of the regression line.



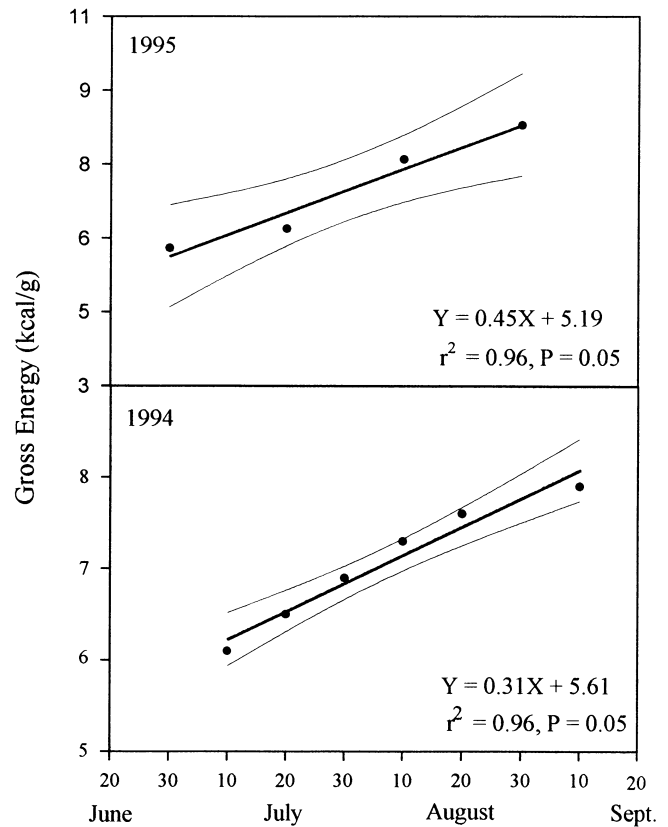
Mean lipid content for male and female moths was 56 and 59% in July, approximately 62 and 69% in August, and 61 and 72% in September, respectively.

High lipid levels in late summer may indicate preparation for migration back to the Plains. Flight is energetically demanding, and the primary flight fuel in lepidopterans is lipid (Weis-Fogh 1952; Gilbert 1967; Mason et al. 1990). The lower whole-body lipid levels in moths captured on the Plains in late summer or early autumn support this hypothesis. Examples of other lepidopterans that accumulate lipid prior to migration include the monarch butterfly, *Danaus plexippus* (Beall 1948), bogong moth, *Agrotis infusa* (Common 1954), *Pseudoplusia includens* (Mason et al. 1989), and green cloverworm, *Plathypena scabra* (Mason et al. 1990).

The seasonal decline in crude protein content is somewhat misleading. Crude protein, which presumably represents flight muscle, was at an essentially constant level throughout the summer, but as moths gained body mass, the proportion of dry mass consisting of crude protein decreased.

The large differences between total moisture level of moths captured on the Plains could be explained by the different amounts of time moths spent in the traps. The traps, which contained no water, were exposed to direct solar radiation and undoubtedly reached high temperatures during the day. Continued dehydration of moths would be expected as long as a moth occupied a trap.

Fig. 6. Gross energy content of army cutworm moths captured at a light trap (elevation 2150 m) located adjacent to an alpine moth aggregation site in Glacier National Park, Montana, 1994–1995. The curved lines denote the 95% confidence interval of the regression line.



Total lipid content of moths captured on the Plains was higher in 1994 than in 1995. Moths left the alpine zone of GNP in late summer of 1994 with approximately 15% more whole-body lipid than in 1995. This could indicate increased moth foraging opportunities as a result of more nights with favorable weather conditions. During rainy or excessively windy nights, army cutworm moths generally did not leave their talus refugia (D. White, Jr., personal observation). Moths captured in 1994 may have also begun their fall migration from a location closer to our Plains study sites than the moths captured in 1995 and simply had more lipid in reserve.

Migration potential

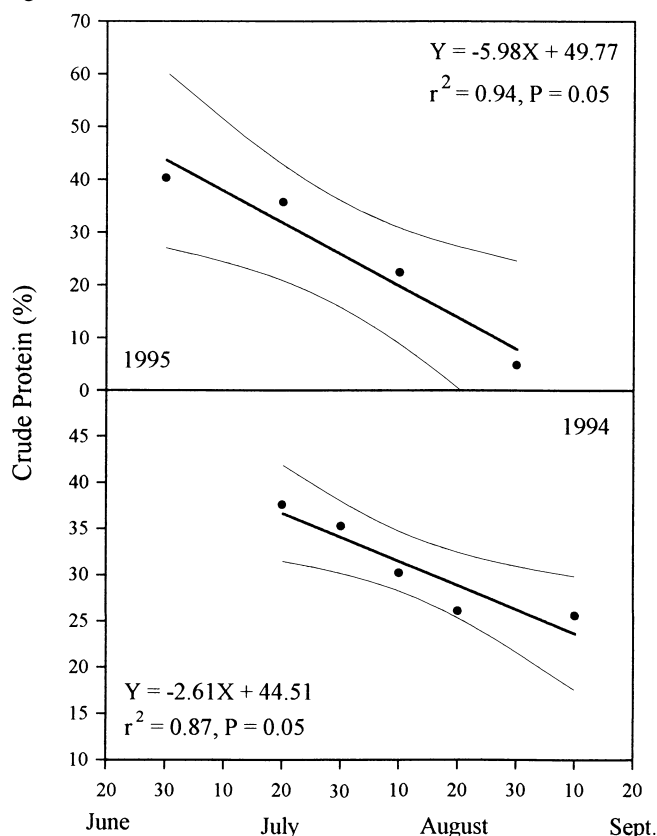
By using a flight mill to determine flight range, Koerwitz and Pruess (1964) demonstrated that army cutworm moths are physically capable of making migratory flights from the Great Plains to the northern Rocky Mountains. By feeding the moths in their study a honey–water solution prior to each flight episode, Koerwitz and Pruess (1964) showed that army cutworm moths could fly up to 300 km in about 65 h. They reported that single flights of 80 km were not unusual; the longest single flight they recorded was 214 km. Periodic food availability is necessary for extensive migrations; unfed and newly emerged moths made only short single flights of less than 8 km before exhaustion occurred (Koerwitz and Pruess 1964).

Table 1. Chemical composition of adult army cutworm moths collected in 2 counties in west-central Montana, 1994–1995.

	Liberty Co.								Ponderosa Co. (1995)			
	1994				1995							
	TM	TN	TL	GE	TM	TN	TL	GE	TM	TN	TL	GE
Sept. 1	—	—	—	—	47	—	—	5.9	42	—	—	6
Sept. 10	6.4	—	28	3.4	—	—	—	—	—	—	—	—
Sept. 20	8.1	—	18	3.1	52	12	11	5.3	65	12	8.8	5.5
Sept. 30	6.9	—	—	5.1	—	—	—	—	—	—	—	—

Note: TM, total moisture; TN, total nitrogen (crude protein); TL, total lipid; GE, gross energy (kcal/g). Values for TM, TN, and TL are percentages based on dry mass of moths.

Fig. 7. Crude protein content of army cutworm moths captured at a light trap (elevation 2150 m) located adjacent to an alpine moth aggregation site in Glacier National Park, Montana, 1994–1995. The curved lines denote the 95% confidence interval of the regression line.



Army cutworm moths may be using different strategies to fuel their spring and autumn migrations. The moths used in the study by Koerwitz and Pruess (1964) had only 5–15% whole-body lipid in the spring, which precluded the use of lipids as a primary spring flight fuel. Before migration in the spring, there would be no time to accumulate adequate lipid levels to fuel flight. Migrating army cutworm moths are probably catabolizing sugars collected from flowers visited during migration in the spring (a pay-as-you-go strategy) and lipids

during the autumn migration after they have had opportunity to accumulate adequate lipid levels (a living-off-of-savings strategy).

We calculated that army cutworm moths that remigrate from the alpine zone of GNP in late summer have enough energy stored as lipid to fly approximately 140 km. This falls short of the actual return flight distance if army cutworm moths are migrating several hundred kilometres from the Great Plains in the spring. Several factors may explain this. First, the cost of transport for most species, including the army cutworm moth, are unknown; the estimated cost of transport, an important factor in computing migratory potential, may be overestimated. Secondly, migratory potential has been calculated under the assumption that the moth is flying in still air. In nature, flight into a head wind would increase the cost of transport, whereas flight with a tail wind would decrease the cost.

In late summer or early autumn in GNP, prevailing low-altitude (<500 m above ground surface) westerly and north-westerly winds are common (Bryson and Hare 1974). It is plausible that remigrating cutworm moths utilize these tail winds to reduce the cost of transport and conserve energy stores. Kanz (1977) and Gibo and Pallett (1979) have shown that migration patterns of monarch butterflies correspond to prevailing low-altitude (<500 m) winds across much of the eastern and southern U.S.A. in September and October. Schmidt-Koenig (1979), Gibo and Pallett (1979), and Gibo (1981) have reported monarch butterflies utilizing tail winds at a ground velocity of 50 km/h and altitudes of over 1200 m above ground surface. Furthermore, updrafts can act to reduce the cost of transport by decreasing the metabolic effort required to stay aloft by providing lift (Hill 1976). Unfortunately, a lack of sufficient data about ambient winds during autumn migration and of the ways in which cutworm moths adjust their flight path in response to winds limits our ability to utilize these factors in estimating migratory potential.

The winter range and migration path of army cutworm moths that summer in GNP are unknown. This knowledge is important because although Glacier's national park status protects some of their summering habitat, army cutworm moths spend most of their life cycle on the Plains, one of the most altered biomes in North America. Activity patterns of grizzly bears in GNP, or even its carrying capacity for grizzly bears, could be influenced by events or activities on the Plains.

Why do army cutworm moths occupy alpine talus slopes during summer?

There are at least 3 possible reasons why army cutworm moths occupy talus slopes. First, the rocks provide protection from avian predators. Ravens (*Corvus corax*) commonly landed near foraging bears and picked off moths that took flight when uncovered by bears' digging. We have also observed Clark's nutcrackers (*Nucifraga columbiana*) and gray-crowned rosy finches (*Leucosticte tephrocotis*) eating army cutworms at alpine moth aggregation sites in GNP.

Secondly, talus slopes may aid moth thermoregulation. There was a steep thermal gradient within the talus debris, particularly at midday (White et al. 1998). It was not uncommon for the temperature of the rocks on the surface of a southwest-facing talus slope on a hot August afternoon to reach 30°C. Ten centimetres into the talus the temperature was 10°C lower. At 20 cm depth the temperature was 15°C lower than at the surface. Army cutworm moths may choose the temperature within a talus slope that meets their immediate thermal needs: near the surface in the mornings, deep within the talus in the afternoon, and back at the surface as temperatures decrease in the evening.

A third and fundamental reason for migration to mountainous regions may be related to exploitation of the large summer bloom in alpine environments. Conceivably, the foraging opportunities afforded by migration would allow for larger clutch sizes and higher productivity. Thus, migrant members of a population would contribute more offspring to successive generations than their sedentary counterparts; in time, migratory behavior would become genetically fixed.

Acknowledgments

Funding was provided by the Peter W. Busch Family Foundation, the Glacier National Park Service, the Biological Resources Division—USGS (formerly the National Biological Service), and the Mountain Research Center, Montana State University—Bozeman. Thanks are extended to N. White, M. Richards, P. Hardiman, J. Grossenbacher, J. Cannon, K. Medley, B. Killingsworth, K. Barnette, J. Barringer, B. Brastrup, D. Heaney, and J. Wargo for their fieldwork.

References

- Aune, K., and Kasworm, W. 1989. Final report—east front grizzly studies. Montana Department of Fish, Wildlife and Parks, Helena.
- Beall, G. 1948. The fat content of a butterfly, *Danaus plexippus* Linn., as affected by migration. *Ecology*, **29**: 80–94.
- Bryson, R.A., and F.K. Hare. 1974. The climates of North America. In *World survey of climatology*. Vol. 2. Edited by H.E. Landsberg. Elsevier Scientific Publishing Co., Amsterdam. pp. 1–47.
- Burton, R.L., Starks, K.J., and Peters, D.C. 1980. The army cutworm. Okla. Agric. Exp. Stn. Bull. No. B749.
- Carrara, P.E., and McGimsey, R.G. 1981. The late-neoglaciation histories of the Agassiz and Jackson Glaciers, Glacier National Park, Montana. *Arct. Alp. Res.* **13**: 183–196.
- Caprio, J.M., Cooksey, D.I., Jacobsen, J.S., Nielsen, G.A., and Roche, R.R. 1997. MAPS Atlas version 5.0: a land and climate information system. Montana State University Extension Service, Bozeman.
- Chapman, J.A. 1954. Studies on summit frequenting insects in western Montana. *Ecology*, **35**: 41–49.
- Chapman, J.A., Romer, J.I., and Stark, J. 1955. Ladybird beetle and army cutworm adults as food for grizzly bears in Montana. *Ecology*, **36**: 156–158.
- Common, I.F.B. 1954. A study of the ecology of the adult bogong moth, *Argotis infusa* (Boisd.) (Lepidoptera: Noctuidae), with special reference to its behavior during migration and aestivation. *Aust. J. Zool.* **2**: 223–263.
- Cooley, R.A. 1916. Observations on the life history of the army cutworm, *Chorizagrotis auxiliaris*. *J. Agric. Res.* **6**: 871–881.
- Craighead, J.J., Sumner, J.S., and Scaggs, G.B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Monogr. No. 1, Wildlife-Wildlands Institute, University of Montana Foundation, University of Montana, Missoula.
- Dightman, R.A. 1967. Climate of Glacier National Park. Bull. No. 7, Glacier Natural History Association (revised edition), West Glacier, Mont.
- Finklin, A.I. 1986. A climate handbook for Glacier National Park, with data for Waterton Lakes National Park. U.S. For. Serv. Gen. Tech. Rep. INT-204.
- French, S.P., French, M.G., and Knight, R.R. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. In *Bears—Their Biology and Management: Proceedings of the 9th International Conference on Bear Research and Management*, Missoula, Mont., February 1992. Edited by James Claar and Paul Schullery. Bear Biology Association, University of Tennessee, Knoxville. pp. 389–399.
- Gibo, D.L. 1981. Altitudes attained by migrating monarch butterflies, *Danaus p. plexippus* (Lepidoptera: Danaidae), as reported by glider pilots. *Can. J. Zool.* **59**: 571–572.
- Gibo, D.L., and M.J. Pallett. 1979. Soaring flight of monarch butterflies *Danaus plexippus* (Lepidoptera: Danaidae) during the late summer migration in southern Canada. *Can. J. Zool.* **57**: 1393–1401.
- Gilbert, L.I. 1967. Lipid metabolism and function in insects. *Adv. Insect Physiol.* **4**: 69–211.
- Hardwick, D.F., and Lefkovitch, L.P. 1971. Physical and biotic factors affecting *Euxoa* species abundance in western North America: a regression analysis. *Can. Entomol.* **103**: 1217–1235.
- Hill, R.W. 1976. Comparative physiology of animals: an environmental approach. Harper and Row, Publishers. New York.
- Johnson, S.A. 1905. Cutworms. Colo. Agric. Exp. Stn. Bull. No. 98. pp. 17–22.
- Kanz, J.E. 1977. The orientation of migrant and non-migrant monarch butterflies, *Danaus plexippus* (L.). *Psyche* (Camb.), **84**: 120–141.
- Kendall, D.M. 1981. Bionomics of *Euxoa auxiliaris* Grote (Lepidoptera: Noctuidae) in the Rocky Mountains and comparison with two resident species of alpine moths. M.S. thesis, Colorado State University, Fort Collins.
- Klaver, R.W., Claar, J.J., Rockwell, D.B., Mays, H.R., and Acevedo, C.F. 1986. Grizzly bears, insects, and people: bear management in the McDonald Peak region, Montana. U.S. For. Serv. Gen. Tech. Rep. INT-207. pp. 205–211.
- Koerwitz, F.L., and Pruess, K.P. 1964. Migratory potential of the army cutworm. *J. Kans. Entomol. Soc.* **37**: 234–239.
- Mason, L.J., Johnson, S.J., and Woodring, J.P. 1989. Seasonal and ontogenetic examination of the reproductive biology of *Pseudoplusia includens* (Lepidoptera: Noctuidae). *Environ. Entomol.* **18**: 980–985.
- Mason, L.J., Johnson, S.J., and Woodring, J.P. 1990. Influence of age and season on whole-body lipid content of *Plathypena scabra* (Lepidoptera: Noctuidae). *Environ. Entomol.* **19**: 1259–1262.
- Mattson, D.J., Gillin, C.M., Benson, S.A., and Knight, R.R. 1991. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Can. J. Zool.* **69**: 2430–2435.
- Morrill, W. 1991. Montana small grain insects: armyworms and cutworms. Montana Agriculture Experiment Station, Montana State University, Capsule Information Ser. No. 34, October 1991.
- O'Brien, S.L., and Lindzey, F.L. 1994. Grizzly bear use of alpine

- insect aggregation sites, Absaroka Mountains, Wyoming. Wyoming Cooperative Fish and Wildlife Research Unit Annual Report, Laramie.
- Pepper, J.H. 1932. Observations on a unidirectional flight of army cutworm moths and their possible bearing on aestivation. *Can. Entomol.* **64**: 241–242.
- Pruess, K.P. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaris* (Lepidoptera: Noctuidae). I. Evidence for migration. *Ann. Entomol. Soc. Am.* **60**: 910–921.
- Schmidt-Koenig, K. 1979. Directions of migrating monarch butterflies (*Danaus plexippus*; Danaidae; Lepidoptera) in some parts of the eastern United States. *Behav. Processes*, **4**: 73–78.
- Schmidt-Nielsen, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science* (Washington, D.C.), **177**: 222–228.
- Seamans, H.L. 1927. Forecasting outbreaks of the army cutworm, *Chorizagrotis auxiliaris* Grote. *Entomol. Soc. Ont. Annu. Rep.* No. 58. pp. 76–85.
- Servheen, C.W. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *J. Wildl. Manage.* **47**: 1026–1035.
- Snow, S.J. 1925. Observations on the cutworm, *Euxoa auxiliaris* Grote and its principal parasites. *J. Econ. Entomol.* **18**: 602–609.
- Strickland, E.H. 1916. The army cutworm *Euxoa auxiliaris* Grote. *Can. Dep. Agric. Entomol. Br. Bull. No. 13*. p. 31.
- Sumner, J., and Craighead, J.J. 1973. Grizzly bear habitat survey in the Scapegoat Wilderness, Montana. Montana Cooperative Wildlife Research Unit, Missoula.
- Walkden, H.H. 1950. Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains. U.S. Department of Agriculture Circ. No. 849.
- Weis-Fogh, T. 1952. Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forskål). *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **237**: 1–36.
- White, D., Jr., Kendall, K.C., and Picton, H.D. 1998. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Can. J. Zool.* **76**: 221–227.