



Two grizzly bear studies : moth feeding ecology and male reproductive biology
by Donnell Dee White, Jr

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in
Biological Sciences

Montana State University

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Abstract:

ABSTRACT Grizzly bears (*Ursus arctos horribilis*) consume adult army cutworm moths (*Euxoa auxiliaris*) from late June through mid-September on high elevation talus slopes in Glacier National Park (GNP), Montana. To better understand the importance of cutworm moths to grizzly bears in GNP, I identified the sex and age classes and minimum number of grizzly bears foraging at moth aggregation study sites, documented the timing and use patterns of grizzly bears foraging in these areas, quantified the effects of mountain climber presence on the behavior of foraging grizzly bears, determined temporal abundance patterns of moths at aggregation study sites throughout the summer, and determined body mass, total body moisture, total lipid, gross energy, and total nitrogen of moths collected throughout the summer. A minimum of 36 grizzly bears were observed 106 times feeding at 6 of 9 known army cutworm moth aggregation sites in GNP, from late-June through mid-September, 1992-1995. No bears were observed on moth sites in 1993. Bears fed on moth aggregations disproportionately more at elevations >2561 m, on slopes between 31° - 45° , and on southwest-facing aspects. Lone adult and subadult grizzly bears appear to be underrepresented and overrepresented at the sites, respectively. Seasonal body weight and seasonal whole-body percentages of total moisture, total nitrogen, total lipid, and gross energy, varied linearly as a function of time. Grizzly bears foraging at moth aggregation sites are sensitive to disturbance from mountain climbers. Because alternative high-quality, late summer foods may not be available, human disturbance should be minimized at moth aggregation sites.

I also evaluated testicular growth and seminiferous tubule development, and age of sexual maturity in 20 male grizzly bears killed in Montana and Wyoming between 1978 and 1992. Seminiferous tubule diameter did not differ among the regions of each testicle sampled. Testicle mass was related linearly to age. Seminiferous tubule diameter was related non-linearly to age. Mean testicle mass, volume, and seminiferous tubule diameter were smaller in immature bears than in mature bears. Based upon the presence or absence of spermatozoa in the lumen of the seminiferous tubules, sexual maturity in grizzly bears from the continental United States is attained at approximately 5.5 years of age.

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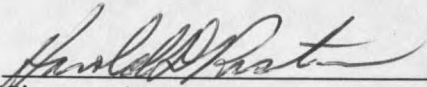
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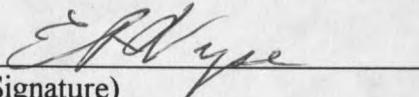
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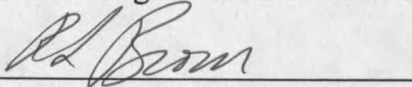
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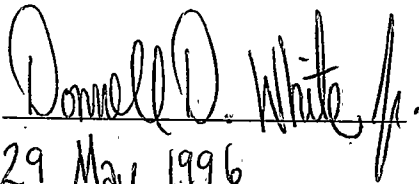

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PREFACE

The grizzly bear (*Ursus arctos horribilis*) in the contiguous United States once ranged from approximately the 100th meridian westward to California and south into Texas and Mexico (Storer and Tevis, 1955). The development of unfavorable environmental conditions in the wake of westward expansion and human development caused a rapid distributional recession (Lewis, 1961; Guilday, 1968). Between 1800 and 1975, grizzly bear populations in the contiguous United States receded from estimates of over 50,000 to less than 1,000 bears (U.S. Fish and Wildlife Service, 1993). Livestock depredation control, habitat deterioration, protection of human life and property, commercial trapping, and sport hunting were leading causes (Stebler, 1972; Martinka, 1976; Brown, 1985).

Currently, grizzly bears occur in less than 2% of their former range south of Canada (U.S. Fish and Wildlife Service 1993). Occupied grizzly bear habitat is largely confined to 5 or 6 areas known to contain either self-perpetuating or remnant populations of bears. These areas include portions of 4 states--Wyoming, Montana, Idaho, and Washington. Grizzly bears may still occur in Colorado, although confirmed sightings have not occurred since 1979 (U.S. Fish and Wildlife Service 1993).

The decreasing numbers and habitat of grizzly bears resulted in the grizzly being listed as threatened under the Endangered Species Act on 28 July 1975. It is important to continue grizzly bear and habitat research to ensure adequate scientific knowledge on which to base conservation and management decisions (U.S. Fish and Wildlife Service 1993).

In an effort to extend our understanding of grizzly bear biology and ecology, I have conducted 2 separate studies focusing on grizzly bear foraging ecology and male reproduction. Therefore, this dissertation is organized into 2 parts. Part A deals with grizzly bear use of high elevation moth aggregation sites in Glacier National Park, Montana, and part B deals with testicular histology of male grizzly bears in Montana and Wyoming.

These studies, like all studies, are not the sole work of their author. I would like to express my appreciation to Michael Kruger, Michelle Richards, Brian Killingsworth, Kimberly Medley, Jeremy Cannon, Piney Hardiman, and Jennifer Grossenbacher for their hard work and assistance in the rugged and remote backcountry of Glacier National Park. Their dedication and spirit of cooperation made the Glacier Park project possible. It was a delight to be in the field with each of them. I also thank Kirk Barnette, Jack Barringer, Bob Brastrup, Dr. Donald Heaney, Darrel Krum, John Maatta, Marko Manoukian, John Maki, Dave Phillips, and Judee Wargo, Montana State University-Bozeman County Agriculture Extension Agents, for collecting army cutworm moths for me in the autumn.

I have benefited both professionally and personally from the opinions, expert advice, and friendship of my major professor Dr. Harold Picton. I also appreciate Dr. James Berardinelli for his willingness to teach me histological techniques and analysis.

I thank my Graduate Committee members, Drs. Lynn Irby, Tom McMahon, Bill Kemp, Gordon Brittan, and Pete Burfening for their willingness to sit on my Graduate Committee and for their time in critically evaluating my dissertation.

I am indebted to Katherine Kendall for asking me to study grizzly bears in Glacier National Park and for entrusting me with this exceptional project. I also thank Matthew Reid for his encouragement and for securing initial funding.

Sincere thanks are extended to Peter Busch, President of the Peter W. Busch Family Foundation, for his friendship and for funding both the Glacier Park and reproductive biology projects. The National Park Service, Glacier National Park, the National Biological Service, the Montana Department of Fish, Wildlife and Parks, and the Mountain Research Center, Montana State University-Bozeman provided additional funding and support; I thank each of them.

Above all, I wish to thank my wife, Nancy. As in my other projects, she participated in every aspect of the work to such an extent that in some ways the results are almost as much hers as mine. She was someone with whom I could discuss concerns, she was also a buffer for disappointments. When at times we had to be apart, my joy in the work diminished and I knew then how much she is the focus of my life.

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ABSTRACT

Grizzly bears (*Ursus arctos horribilis*) consume adult army cutworm moths (*Euxoa auxiliaris*) from late June through mid-September on high elevation talus slopes in Glacier National Park (GNP), Montana. To better understand the importance of cutworm moths to grizzly bears in GNP, I identified the sex and age classes and minimum number of grizzly bears foraging at moth aggregation study sites, documented the timing and use patterns of grizzly bears foraging in these areas, quantified the effects of mountain climber presence on the behavior of foraging grizzly bears, determined temporal abundance patterns of moths at aggregation study sites throughout the summer, and determined body mass, total body moisture, total lipid, gross energy, and total nitrogen of moths collected throughout the summer. A minimum of 36 grizzly bears were observed 106 times feeding at 6 of 9 known army cutworm moth aggregation sites in GNP, from late-June through mid-September, 1992-1995. No bears were observed on moth sites in 1993. Bears fed on moth aggregations disproportionately more at elevations >2561 m, on slopes between 31 - 45°, and on southwest-facing aspects. Lone adult and subadult grizzly bears appear to be underrepresented and overrepresented at the sites, respectively. Seasonal body weight and seasonal whole-body percentages of total moisture, total nitrogen, total lipid, and gross energy, varied linearly as a function of time. Grizzly bears foraging at moth aggregation sites are sensitive to disturbance from mountain climbers. Because alternative high-quality, late summer foods may not be available, human disturbance should be minimized at moth aggregation sites.

I also evaluated testicular growth and seminiferous tubule development, and age of sexual maturity in 20 male grizzly bears killed in Montana and Wyoming between 1978 and 1992. Seminiferous tubule diameter did not differ among the regions of each testicle sampled. Testicle mass was related linearly to age. Seminiferous tubule diameter was related non-linearly to age. Mean testicle mass, volume, and seminiferous tubule diameter were smaller in immature bears than in mature bears. Based upon the presence or absence of spermatozoa in the lumen of the seminiferous tubules, sexual maturity in grizzly bears from the continental United States is attained at approximately 5.5 years of age.

PART A

GRIZZLY BEAR USE OF HIGH ELEVATION MOTH AGGREGATION SITES IN GLACIER NATIONAL PARK, MONTANA

Introduction

Grizzly bears (*Ursus arctos horribilis*) feeding on insect aggregations excavated from alpine talus slopes have been documented in several areas in the northern Rocky Mountains: the Mission Mountains (Chapman 1954, Chapman et al. 1955, Servheen 1983, Klaver et al. 1986), Scapegoat Wilderness (Sumner and Craighead 1973, Craighead et al. 1982), and mountains of the Rocky Mountain East Front (Aune and Kasworm 1989), Montana; and in the Absaroka Mountains, Wyoming (Mattson et al. 1991, French et al. 1994, O'Brien and Lindzey 1994). Grizzly bears consume army cutworm moths (*Euxoa auxiliaris*) (Lepidoptera: Noctuidae) and ladybird beetles (*Coccinella* and *Hippodamia* spp.) (Coleoptera: Coccinellidae) in the Mission Mountains and army cutworm moths in the Scapegoat Wilderness, Rocky Mountain East Front, and Absaroka Mountains. Additionally, Ustinov (1965) has recorded bears eating aggregations of caddis flies (Trichoptera) along the shores of Lake Baikal, Russia, and Gurney (1953) observed bears feeding on fossil grasshoppers (Orthoptera) melted out of glaciers.

Anecdotal accounts of grizzly bears frequenting high elevation (>2000 m) talus slopes in Glacier National Park (GNP), Montana, are common in Park records. The first recorded report of bears observed above timberline in GNP was made by climbers on Mt. Cleveland (3190 m) in 1933. These climbers found "signs of a grizzly within 1000 feet of the summit" and the climbers considered this "the most remarkable thing in the whole trip." Though the climbers were the Chief Naturalist of GNP and a seasonal staff member, they had no plausible explanation for what the bear was doing at that elevation. Moth remains were confirmed in bear feces (scats) collected from several of GNP's tallest mountain peaks in the early to mid-1980's (Katherine C. Kendall, unpub. data).

From 1989 - 1991, 5 radiotelemetered grizzly bears spent several weeks feeding on army cutworm moths at 2100 - 2800 m elevation on mountains along the east side of GNP. These bears initiated feeding on moths as early as the third week of June and continued until mid to late August or early September (Daniel Carney, U.S. Fish and Wildlife Service, Browning, Montana, unpub. data).

In this study, I investigated grizzly bear use of army cutworm moths on high elevation talus slopes in GNP. Prior to my investigation, information on grizzly bear use of army cutworm moths was limited to 4 studies; 3 in the Greater Yellowstone Ecosystem (Mattson et al. 1991; French et al. 1994; O'Brien and Lindzey 1994) and 1 in the Mission Mountains, Montana (Klaver et al. 1986).

My goals were to determine the significance of high elevation army cutworm moth aggregations to the grizzly bear population in Glacier National Park and to quantify what physical, biological, and social parameters influence grizzly bear use of these areas. To meet these goals I pursued 5 specific objectives: (1) to identify the sex and age classes and minimum number of grizzly bears foraging at moth aggregation study sites, (2) to document the timing and use patterns of grizzly bears foraging in these areas, (3) to determine temporal abundance patterns of moths at aggregation study sites throughout the summer, (4) to determine total moisture, total nitrogen, total lipid, gross energy, and body mass of moths collected throughout the summer and early autumn, and (5) to quantify the effects of mountain climber presence on the behavior of foraging grizzly bears.

Life History Of The Army Cutworm Moth

The army cutworm moth is distributed throughout the semiarid region of the Great Plains, extending as far east as Kansas, south to southern New Mexico, west to California, and north to central Alberta (Fig. 1). Since 1929, the army cutworm has been reported in all states west of the Mississippi River except Louisiana (Burton et al. 1980). The army cutworm moth is also widespread throughout Alberta and is commonly abundant as far north as the Peace River District (Strickland 1942, Burton et al. 1980).

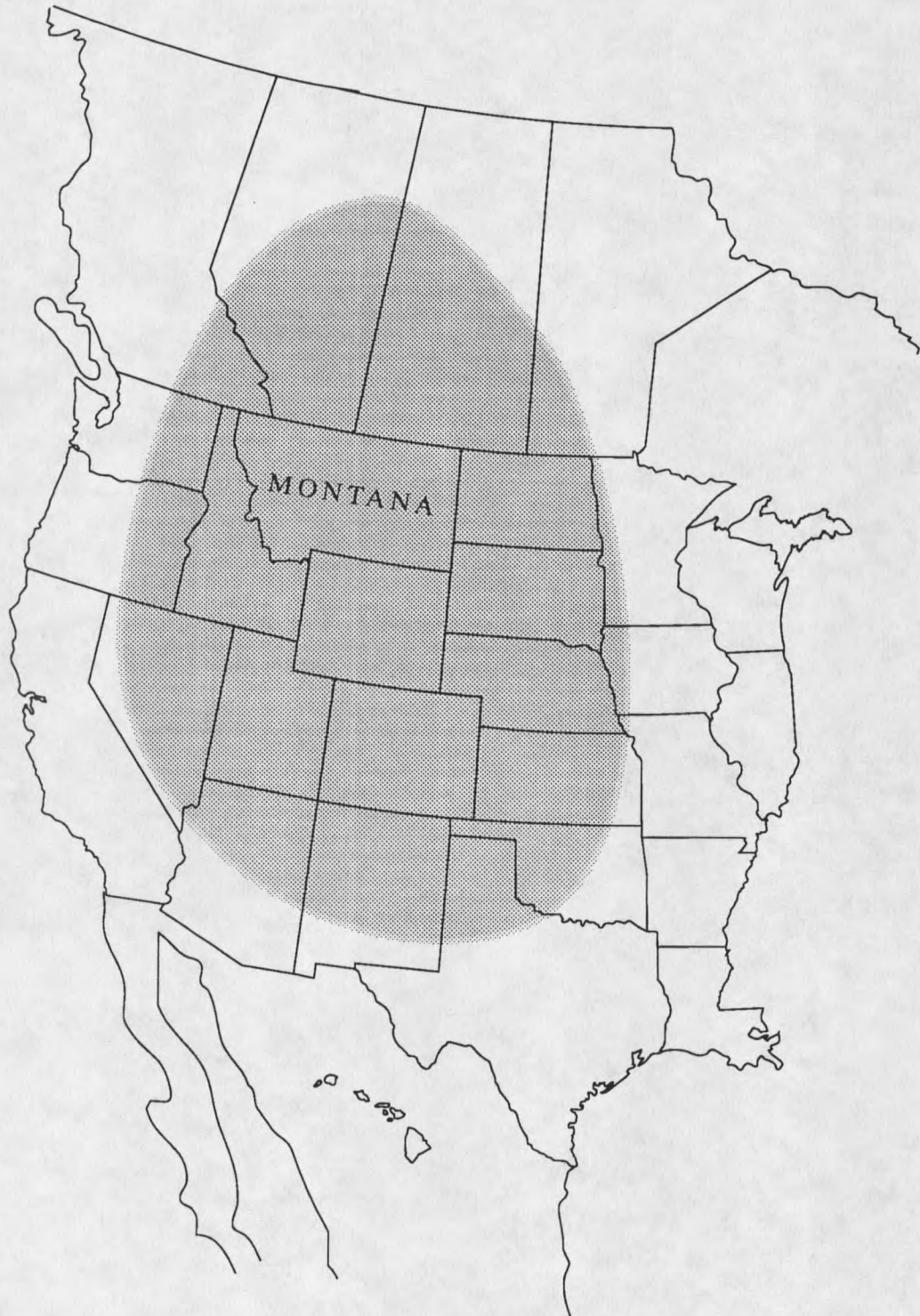


Figure 1. Distribution of the army cutworm moth in North America. Modified from Burton et al. (1980).

The life history of the army cutworm moth is remarkable and required decades for biologists to piece together. Because of the abundance of the moths in the spring and autumn on the Great Plains, Gillette (1904) and Johnson (1905) incorrectly proposed that the army cutworm moth was bivoltine. Cooley (1916) reared army cutworm moths in outdoor cages on the Plains during the summer in Montana, but few individuals survived. This led Cook (1927) to propose that adult army cutworm moths aestivated (i.e., were inactive) under matted vegetation and other debris on the Plains to escape the heat of summer. This "heat-escape hypothesis" also explained why army cutworm moths vanished during summer on the Plains. Simple but elegant experiments conducted by Pepper (1932) determined that army cutworm moths could be kept alive during the summer on the Plains by storing them at cool temperatures.

In May of this same year, Pepper (1932) observed a swarm of army cutworm moths flying southwesterly near Bozeman, Montana. Pepper was the first to hypothesize that these moths migrated to high elevations for the summer. Pruess (1967) developed a more detailed and cohesive theory of army cutworm moth migration based on 4 observations: 1) the absence of adult army cutworm moths on the Plains during the summer in Nebraska, 2) the long distance flight ability of this moth (as demonstrated by experimentation in the mid-1960's), 3) numerous records of the moths at high elevations during the summer, and 4) moths captured on the Plains in the autumn had higher body fat reserves than those collected in spring indicating that they fed during the summer and did not aestivate as previously accepted. Pruess

and Pruess (1971) further documented nocturnal unidirectional migration of army cutworm moths at North Platte, Nebraska, and Laramie, Wyoming, using telescopes focused on the moon.

This and the work that has followed has clarified the life history of this complex animal (Fig. 2). The army cutworm moth is holometabolous. The eggs are laid in the

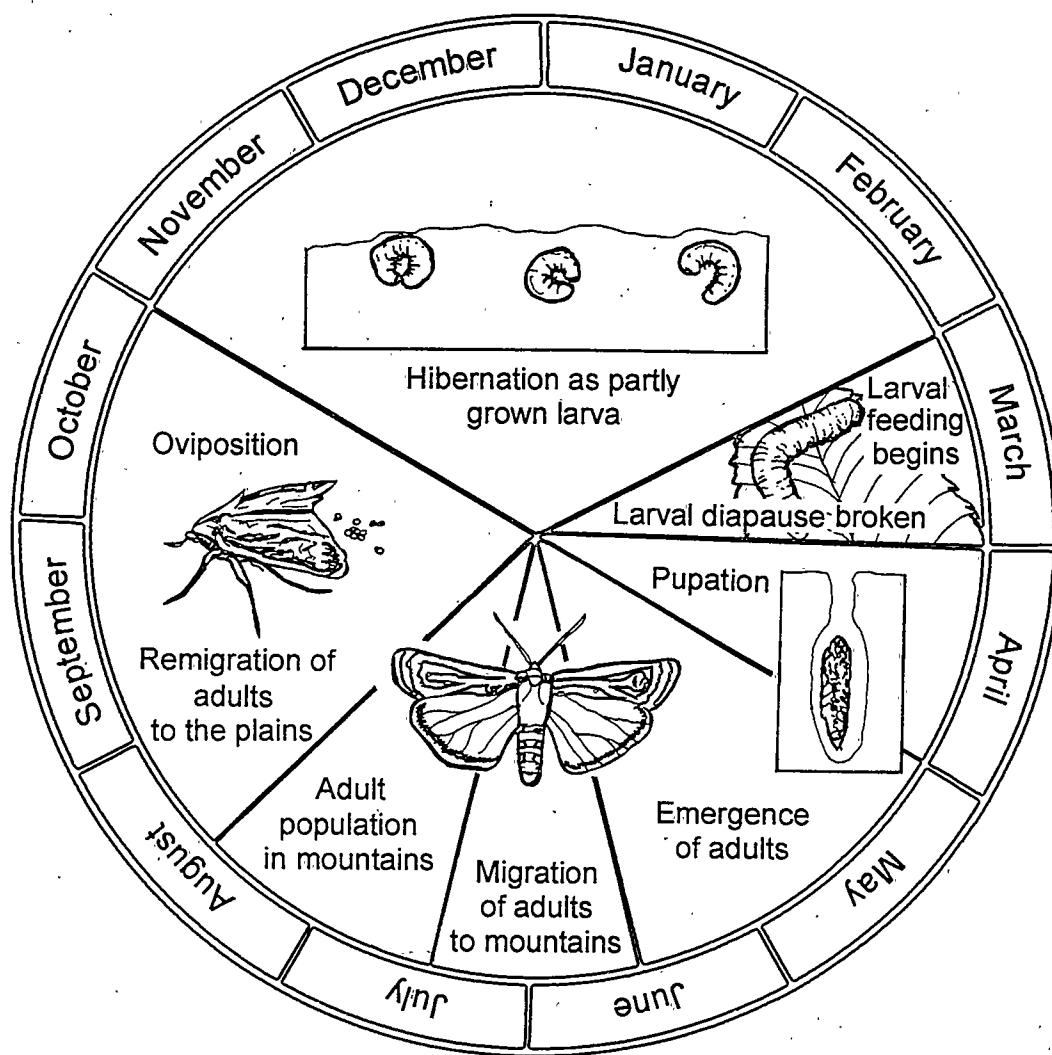


Figure 2. The life cycle of the army cutworm moth. Redrawn from Kendall 1981.

soil of the Great Plains in the autumn and develop to the first or second larval instar before hibernation (Johnson 1905, Cooley 1916, Strickland 1916, Burton et al. 1980, D. Kendall 1981). In spring, the larvae commence to feed on a variety of plants such as alfalfa and small grains (Burton et al. 1980, Morrill 1991). If development is not interrupted by low temperatures and the larva continue to feed, the larval stage may last for only 10 days (Rockburne and Lafontaine 1976). The larval stage can, however, last longer: 25 to 32 days in Kansas (Walkden 1950) and 43 to 63 days in Montana (Cooley 1916). When abundant and short of food, the larvae will move *en masse* to adjacent fields, thus the name "army" cutworm. 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 early summer the newly emerged adult moths enter a migratory phase and fly west into the Rocky Mountains (Pepper 1932, Walken 1950, Chapman et al. 1955, Pruess 1967, Hardwick and Lefkovitch 1971, Burton et al. 1980) where they spend the summer. It is here, while inhabiting the interstia of talus slopes that the moths are excavated and consumed by grizzly bears. They do not become reproductively active until autumn when they return to the plains. On the plains the females enter a settling phase and oviposit approximately 2000 eggs per individual into the soil (Walkden 1950, Burton et al. 1980). The army cutworm moth is univoltine (Cooley 1908, Seamans 1927, Burton et al. 1980, Kendall 1981).

Definitions

Several terms used loosely in the ecological literature are defined below to clarify my use of the terms:

1. Migration is the act of moving from one spatial unit to another (Baker 1982).
2. Remigration is the act of migrating to a spatial unit that is environmentally similar to a spatial unit that has been visited before.
3. Movement is defined as simply a change in position.

Study Area

GNP is located in northwestern Montana adjacent to the Canadian border (Fig. 3). Two mountain ranges dominate the park: the Livingston Range, located on the west side of the park, extends north from the Canadian border southward to Lake McDonald; and the Lewis Range, on the east side, extends the entire length of the park. The continental divide bisects the park following the crest of the Lewis Range northward to about 18 km south of the Canadian border where it turns westward to follow the crest of the Livingston Range into Canada (Carrara and McGimsey 1981). About one third of GNP's 410,000 ha occurs above timberline. Much of the remainder of the park 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 948 m at

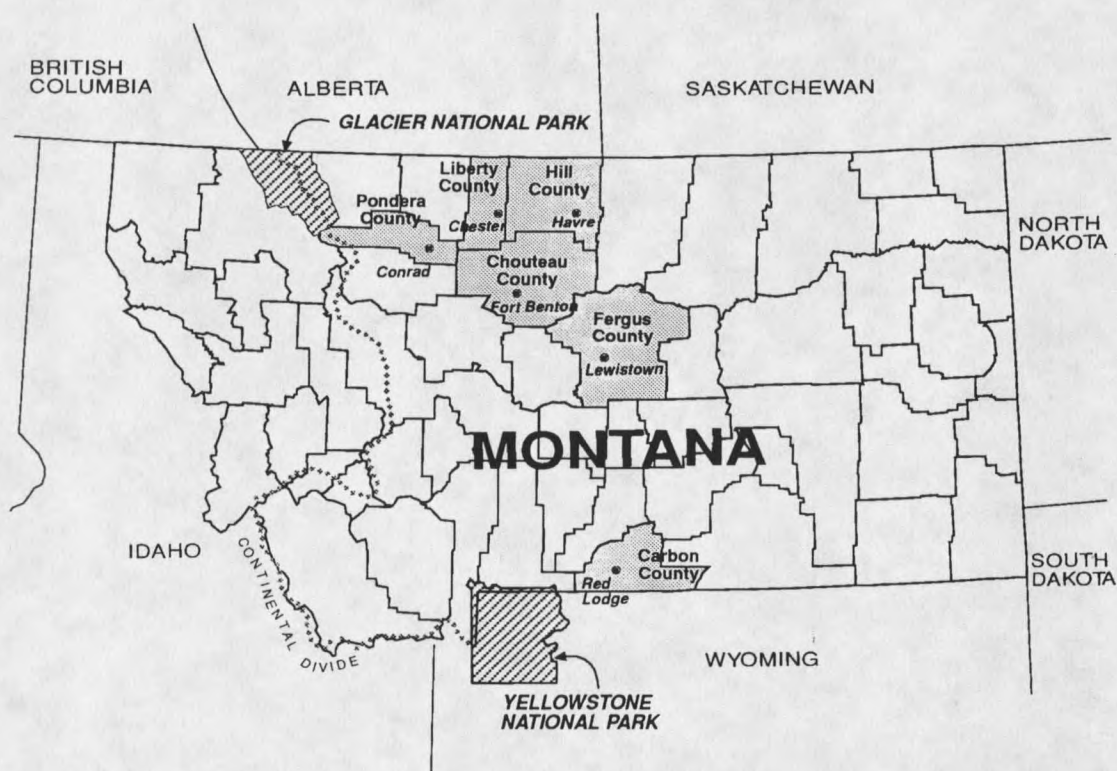


Figure 3. Location map of Glacier National Park, Montana and the location of counties in Montana (shaded areas) where adult army cutworm moths were collected in late summer and early autumn, 1992-1995.

the Middle Fork-North Fork Flathead River confluence to 3,190 m atop Mount Cleveland (Finklin 1986).

The mountains of GNP presumably originated with the uplift and folding of sedimentary rocks of the Precambrian Belt Supergroup during the late Mesozoic. These strata are mostly reddish brown and greenish gray argillites with some quartzites (Carrara and McGimsey 1981). Glaciers shaped the terrain to its present appearance during the Pleistocene (Alden 1953, Dyson 1966, Alt and Hyndman 1991).

The climate 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 near and beyond the eastern edge of the park (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 to 8°C per 1000 m (Finklin 1986).

Methods

Moth Site Characteristics

I visited 7 alpine moth aggregation sites in GNP before, during, and after seasonal bear use, which occurred from late June to mid-September. Data collected at moth aggregation sites included measurements and descriptions of site characteristics (e.g., elevation, slope, aspect) and bear sign (e.g., dig dimensions and dig-site features, bed dimensions and locations).

To quantify the thermal environment of a talus slope, I placed automatic temperature loggers (HOBO TEMP, Onset Computer Corporation, Pocasset, MA) programmed to measure temperature every 30 minutes for 36 days at the surface and

at 3 depths within a southwest-facing talus slope: 10 cm, 20 cm and 30 cm. The thermometers were buried 3 August 1995 and removed 10 September 1995.

Bear Observation Techniques

I observed bear foraging activity at alpine moth aggregation sites using variable power spotting scopes or telescopes at distances of 250 m to 2 km. Moth aggregation study sites were chosen for observability and accessibility, intensity of bear use, minimal bear disturbance by researchers, and researcher safety. Observation posts were chosen on the basis of bear observability and bear avoidance, researcher concealment, and prevailing wind direction. Bears were identified as to species and sex/age classes using established guidelines for field identification of bears (Burkholder 1959, Meehan 1961, Woodgerd 1964, Craighead et al. 1974, Martinka 1974, Egbert and Stokes 1976, Atwell et al. 1980, French et al. 1994, O'Brien and Lindzey 1994). Subadults were distinguished by size and relative body proportions.

Repeated observations of the same bears on a talus slope allowed me to identify many bears individually. Pelage color and shedding patterns, size, conformation, and deformities were the distinguishing characteristics used. Sex, age, family groupings, and behavior traits were used as distinguishing factors, which led to a high confidence in the identification of individuals. Location of each bear observed foraging on moths was recorded on U.S. Geological Service 7.5 minute series topographic maps using Universal Transverse Mercator (UTM) coordinates.

Bear Activity Budgets

I determined activity budgets during moth feeding episodes using behavior scans during direct observations and by reviewing 16 mm film records. Moth aggregation sites were scanned for a 15 minute time period for each hour of observation to determine the activity patterns of adult female, lone adult, and subadult grizzly bears observed feeding on moths. At 10 second intervals throughout the 15 minute sampling period, the category of activity of a focal bear was recorded (Altmann 1974). Behaviors were classified as: foraging on moths, moving, sleeping, loafing-awake, foraging on vegetation, nursing, and defense (i.e., head down and swaying back and forth, ears laid back on sides of head, charges, etc.). The percent occurrence for a given behavior was determined by dividing the number of instantaneous observations recorded for that behavior by the total number of behavioral observations. Other data collected included number, temporal use patterns, and intraspecific behavioral interactions.

Scat Analysis

Bear scats were collected from moth aggregation sites and their locations (UTM coordinates) recorded. Scats were analyzed for percent frequency, volume, and ingested volume of items consumed. Percent volume ingested was estimated by using correction indexes for differential digestibility of items (Hewitt 1989). These methods were the same as described by Mattson et al. (1991).

Moth Capture Techniques

I used 3 different methods to collect moths. A standard blacklight trap using an 8 watt Sylvania F8T5/BL fluorescent tube was the primary method used in the alpine to capture moths from late June through early September, 1994 and 1995. Each blacklight was powered by a 12 volt DC marine battery. The number of moths captured per trap night was used as an index to moth abundance on moth aggregation sites throughout the summer. The killing agent was 10% formaldehyde and detergent. Traps were equipped with automatic light switches. Traps were emptied and a fresh battery exchanged approximately every 14 days.

Moths were also excavated in the alpine by hand from 1 talus slope on 15 August 1992, 17 August 1994 and 21 August 1995. A 40 m x 40 m grid was established each year using a 10 m-long rope. Sixteen sampling stations with an area of 0.25 m² each were established and the number of moths were determined at each station each year. The talus was excavated until sandy soil or snow/ice prohibited digging further. Most of the moths were located within the top 15 cm. In 1992, I visually selected 5 areas on the talus slope where density of moths appeared to be especially high and sampled these areas using the same method.

To compare nutritional composition of moths captured in the alpine of GNP with moths captured during remigration on the plains, sex-attractant traps (Unitrap, Phero Tech. Inc. British Columbia, Canada) baited with army cutworm lure (Terochem Laboratories LTD, Edmonton, Alberta, Canada) were used in 6 counties of north and

south-central Montana in late summer and early autumn (mid-August to mid-October or early November) (Fig. 3). Prior to placement in the field each trap was positioned near the top of a wood stake (approximately 120 by 4 by 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 air flow pattern were avoided. At the trap site, the stake with the attached trap was driven into the ground to a depth such 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 was conducted by Montana State University-Bozeman Agriculture Extension Agents.

Nutritional Analysis Of Moths

To assess the nutritional benefits of moth foraging by grizzly bears, gross energy and total nitrogen (crude protein) were determined on moths collected with bomb calorimetry and macro-Kjeldahl methods, respectively. Total lipid (ether extract) was also estimated using a Soxhlet apparatus and total moisture was determined via weight difference before and after drying. Except for total moisture, nutritional analyses are reported on a dry weight basis. Moths were stored frozen in dry sealed containers to minimize dehydration prior to analysis. At least 20 moths were used for each analysis for each date. All analyses were conducted at the Analytical Laboratory, Montana State University-Bozeman.

To determine the number of moths a bear could potentially consume in a day, I multiplied the mean number of moths in a bear scat taken from a moth site by the mean number of times a bear defecated in a day. Since little or no moth foraging occurred at night or before 0600, a day here refers to the 16 hour observation period bears were observable on a moth site.

Bear Disturbance

On 7 separate occasions, I observed mountain climbers disturb grizzly bears as the bears fed at moth aggregation sites. Potential effects of disturbance was quantified by conducting activity budgets on bears as they reacted to climber presence.

Statistical Analysis

I used the log-likelihood ratio (G) to test goodness of fit between observed and expected frequencies (Zar 1984) of bear sightings among bear sex and age classes and elevation, aspect, and slope classes. Bonferroni confidence intervals were calculated to determine which classes differed significantly between observed and expected values (Byers et al. 1984), given a significant difference in overall frequency distributions. The expected distribution of sightings among bear classes was derived from GNP employee bear sighting reports accumulated from January 1967 through December 1994 (Katherine C. Kendall, pers. commun., 1995). Lone adults, subadults, females with cubs of the year, and females with yearling or 2.5 year old cubs

comprised 60.5, 13.4, 14.4, and 11.7%, respectively, of 4576 bear observations made during this time period. Expected distributions of observations for elevation, aspect, and slope classes were derived for 20,000 random points using the geographical information system digital elevation model for GNP. Random point determination was restricted to areas above 2141 m, the minimum elevation of documented sites of bears feeding on moths. Seasonal changes in nutritional content of moths was analyzed using least-squares linear regression. In all analyses performed, I accepted Alpha \leq 0.05 as significant.

Results

Moth Site Characteristics

I identified a total of 9 sites used by bears to feed on army cutworm moth aggregations. I visited 7 of these sites a total of 38 times from 1992 to 1995. Seven sites were located in glacial cirques on talus slopes immediately below steeper headwalls, 2 sites were at or near the summits of their respective massifs. The talus slopes at the sites I visited were active and deposition of rock debris commonly occurred during my visits, particularly in the early morning hours (0400 - 0600). None of the talus interstia were filled with debris. The angular rocks of the talus slopes ranged from 2 to \geq 100 cm in size. Elevations at the 9 sites averaged 2621 ± 198 m (2141- 3129 m), and slopes were $37 \pm 9.5^\circ$ (8 - 66°). Five of the sites were on south aspects, and 4 were on western aspects.

Talus slopes used for feeding by bears were essentially devoid of vegetation except for strings of vegetation associated with water seepage areas; even the lichen cover on rocks was sparse. As the moth sites were located at or near the summits of their associated massifs, few alpine tundra-covered benches occurred above the moth sites. Below the moth sites, however, plateaus and benches occurred and were dominated by forbs, most commonly *Erythronium grandiflorum*, *Polygonum bistortoides*, and *Dryas hookeriana*. Graminoids, including *Poa* spp. and *Carex* spp. were also common on these moister, lower elevation benches.

Temperatures of talus slopes varied widely with depth. Mean surface temperatures of a southwest-facing talus slope (2300 m) during 3 August-10 September 1995 fluctuated widely (e.g., 3-22°C), reaching 22 °C in the early afternoon (Fig. 4). At 30 cm deep into the talus debris, however, temperature fluctuations were much reduced, ranging only a few degrees daily (Fig. 4), and averaging about 5°C over a 24 hour period.

Bear Use Of Moth Sites

Cutworm moths predominated the diet of bears occupying talus slopes. I observed a minimum of 36 different grizzly bears feeding at 6 of 9 known moth aggregation sites in GNP from late-June through mid-September, 1992 - 1995 (Table 1). No bears were observed on moth sites in 1993. Subadults, lone adults, adult females with cubs of the year, and adult females with yearling cubs were observed. Of 106 total bear

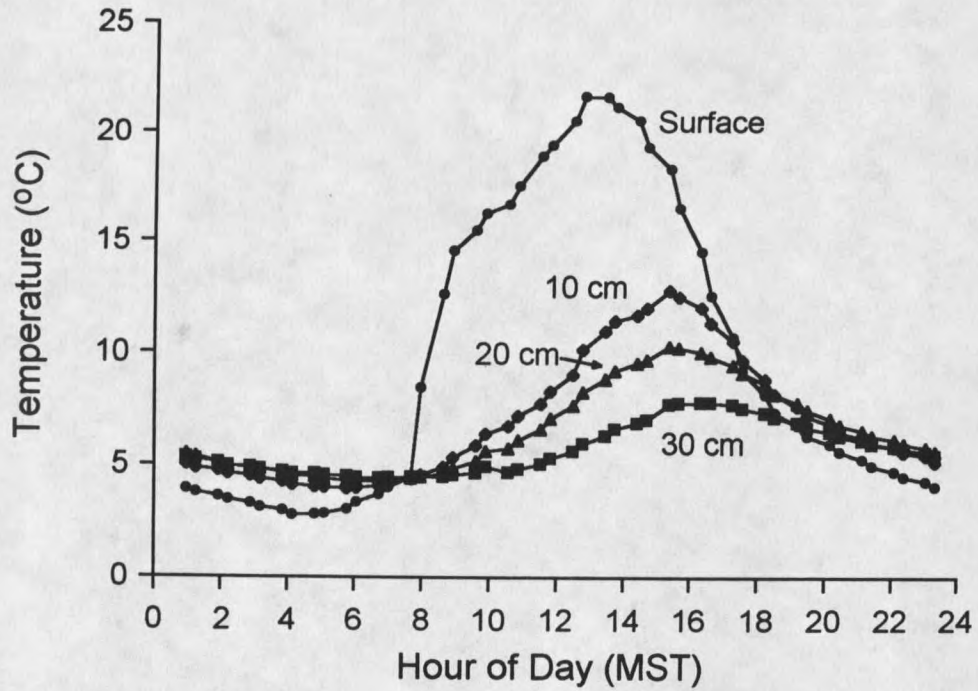


Figure 4. Temperatures on the surface and at 10, 20, and 30 cm depths within a southwest-facing talus slope (2150 m) in Glacier National Park, Montana, 3 August-10 September, 1995. MST = Mountain Standard Time.

observations (family groups were counted as a single observation), no black bears (*U. americanus*) were observed.

Table 1. Minimum number of different grizzly bears observed on moth aggregation sites in Glacier National Park, Montana, 1992, 1994-1995*.

Moth Site	<i>n</i>	RF ^a	C ^b	Y1 ^c	Y2 ^d	SA ^e	LA ^f
Twin Peaks	16	4	3	3	1	0	5
Two Medicine	4	1	1	1	0	0	1
Northern Exposure	4	1	3	0	0	0	0
Pinchot Creek	6	1	1	0	0	0	4
Medicine Grizzly	3	1	0	1	0	0	1
Triple Divide	3	0	0	0	0	3	0
	36	8	8	5	1	3	11

*Only 2 bears (a female and a 1.5 year old cub) in 1994 and 3 bears (a female and 2 1.5 year old cubs) in 1995 were observed on moth sites.

^aRF = reproductive females (i.e., females accompanied by cubs).

^bC = cubs-of-the-year.

^cY1 = 1.5 year old cubs.

^dY2 = 2.5 year old cubs.

^eSA = subadults.

^fLA = lone adults.

Frequencies of observed and expected grizzly bear classes differed significantly ($G = 19.80$, $df = 3$, $P < 0.05$) (Table 2). This difference was attributable to overrepresentation of subadults and underrepresentation of lone adults. The frequency of observations among bear classes did not differ ($G = 0.17$, $df = 2$, $P = 0.92$) between the time periods analyzed (15 June - 15 July, 16 July - 15 August, 16 August - 15 September) (Table 3).

Table 2. Observed and expected numbers of grizzly bears at moth aggregation sites in Glacier National Park, Montana, 1992-1995.

	Observed	Population expected
Subadult	31 a	13 b
Lone adult	34 a	65 b
Female with cub(s) of year	24 a	15 a
Female with yearling(s)	17 a	13 a

Values in rows followed by a different letter are significantly different ($P < 0.05$).

Table 3. Number of grizzly bear observations and proportionate representation of bear classes at moth aggregation sites in Glacier National Park, Montana, 1992-1995.

	No. of bear observations	Bear class proportion		
		Subadults	Lone adults	Females with young
15 June - 15 July	18	0.333*	0.333*	0.333*
16 July - 15 August	48	0.33	0.35	0.31
16 August - 15 September	40	0.3	0.35	0.35

Values are proportions of total bear observations, by time period.

*Sample sizes <24.

Based upon examination of 280 bear scats collected from moth aggregation sites in 1992, 1994, and 1995, bears ate mainly army cutworm moths (Table 4). Moths appear to be highly digestible; essentially all moth parts are digested except for their exoskeletons. Graminoids were also eaten, particularly, *Poa* spp. and *Carex* spp., but little grazing was observed in adjacent mesic areas.

Table 4. Average content of bear scats ($n = 280$) collected at moth aggregation sites in 1992 - 1994 in Glacier National Park, Montana.

	% Frequency	% Volume	% Ingested Volume ^a
Moths	78.3	67.2	95.2
Debris (mostly rocks)	58.4	16.3	-----
Grass/Sedge	23.1	15.3	3.8
Ants (Formicidae)	5.8	0.9	0.9
<i>Vaccinium globulare</i>	6.5	0.3	0.1

^aIngested volume was estimated by applying correction factors of Hewitt (1989), excluding debris.

Bear excavations were oval in shape and 0.1 - 0.8 m, typically 0.2 - 0.5 m deep. Mean total volume of talus debris excavated for 30 pits was 0.22 m³. When 2 or more bears or family groups fed at a moth site, they were separated by 50 - 100 m, with the exception of paired subadults. Bear use was concentrated within areas of about 200 x 200 m. I found up to 100+ scats in these areas; others were undoubtedly covered as bears dug. Bears observed digging for moths ($n = 106$) were not distributed randomly with respect to elevation, slope, or aspect (Fig. 5).

Fifteen bedding sites were found at 3 moth sites. These beds were excavated in the open talus feeding sites ($n = 5$) or adjacent to large boulders ($n = 10$). These beds were typically shallow depressions (0.05 - 0.1 m) shaped from scree or snow. Few scats were found around the beds.

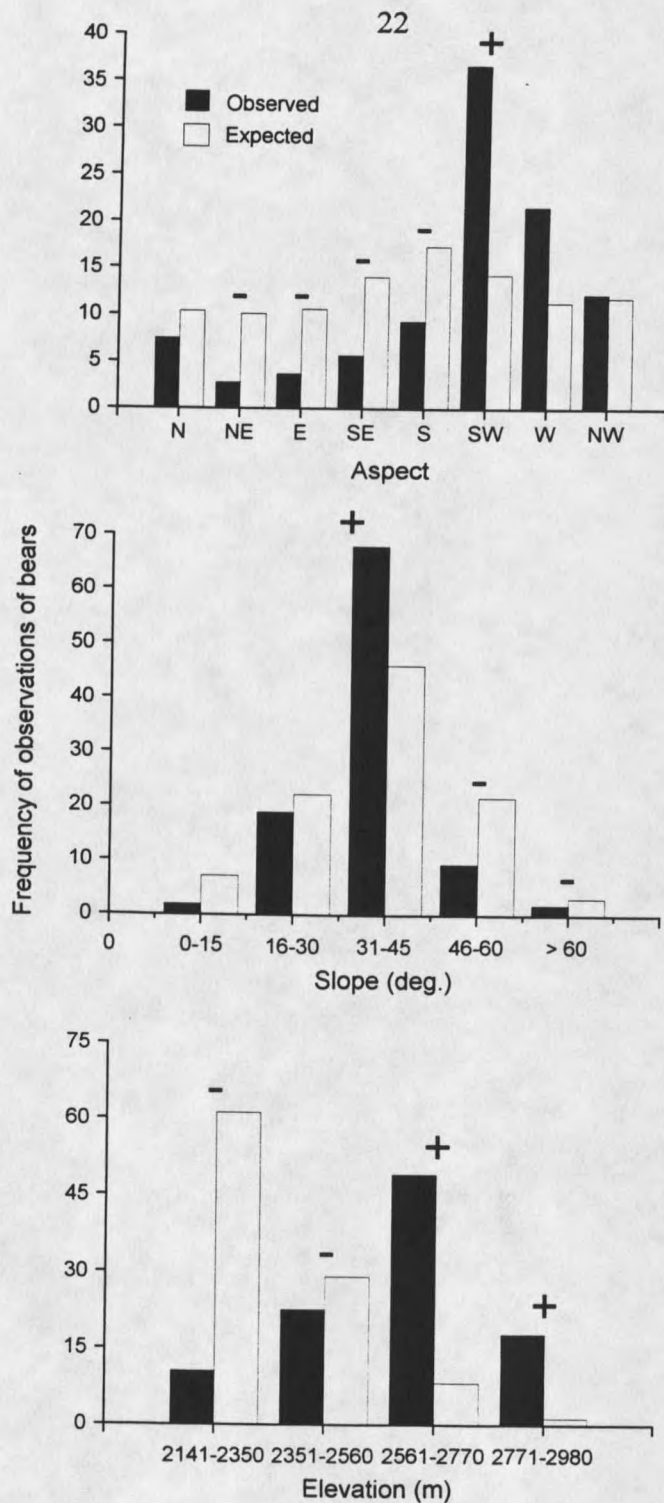


Figure 5. Observed and expected frequencies of individual grizzly bears or family groups excavating for army cutworm moths in Glacier National Park, Montana, by elevation (bottom), slope (middle) and aspect (top). A plus sign denotes observed frequencies significantly greater or less than expected, respectively ($P < 0.05$).

Bear Activity Patterns

I determined the type of activity engaged in by 18 adult grizzly bears for 104 15-minute intervals. Bears foraged heavily on moths from 0600 - 1200, commonly sleeping on site between 1300 - 1800, then foraging for moths again in the early evening (Fig. 6). While foraging for moths, a bear typically stayed in 1 location for up

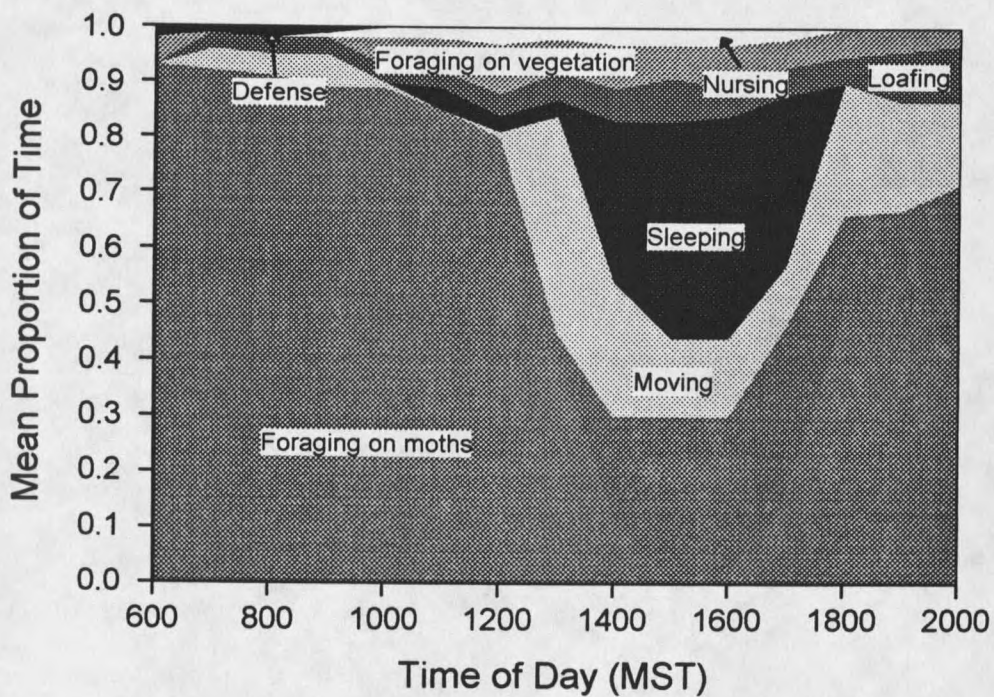


Figure 6. Diurnal activity patterns of 18 adult grizzly bears relative to time of day on moth aggregation sites in Glacier National Park, Montana, 1992, and 1994-1995. MST = Mountain Standard Time.

to 15 minutes before moving to a new location, which was usually within a 1-2 m of the previous excavation. A mean of 67% of each day was spent foraging for moths.

Moving on, off, or within the site tended to be more common after 1200. Little movement of the bears occurred before 1200. Defensive behaviors were observed only during the early morning hours (Fig. 6).

The amount of time during the summer devoted to moth foraging varied widely among bears observed. I observed 1 female with a yearling cub use 1 moth aggregation site for at least 32 days. Five lone adults were observed foraging for moths on 3 different moth aggregation sites for at least 28, 25, 22, 21, and 20 days each. Two females with cubs-of-the-year were observed for only 3 days each. Because it was not possible to observe every moth aggregation site every day, these numbers should be considered conservative estimates of the length of time grizzly bears utilize moth aggregation sites in GNP.

Chronology Of Moth Migrations

Army cutworms moths arrived in the alpine of GNP in early July in 1994 and in late June in 1995 (Fig. 7). Moth abundance peaked in late July in 1994 and in mid July in 1995. I did not capture any army cutworm moths after 10 August in 1994 or after 30 July in 1995 (Fig. 7).

The earliest moths were captured on the plains was in early August in Pondera County, Montana (Fig. 8). Peak seasonal abundance, however, did not normally occur until after the first week of September in most years in Pondera, Chouteau, Liberty,

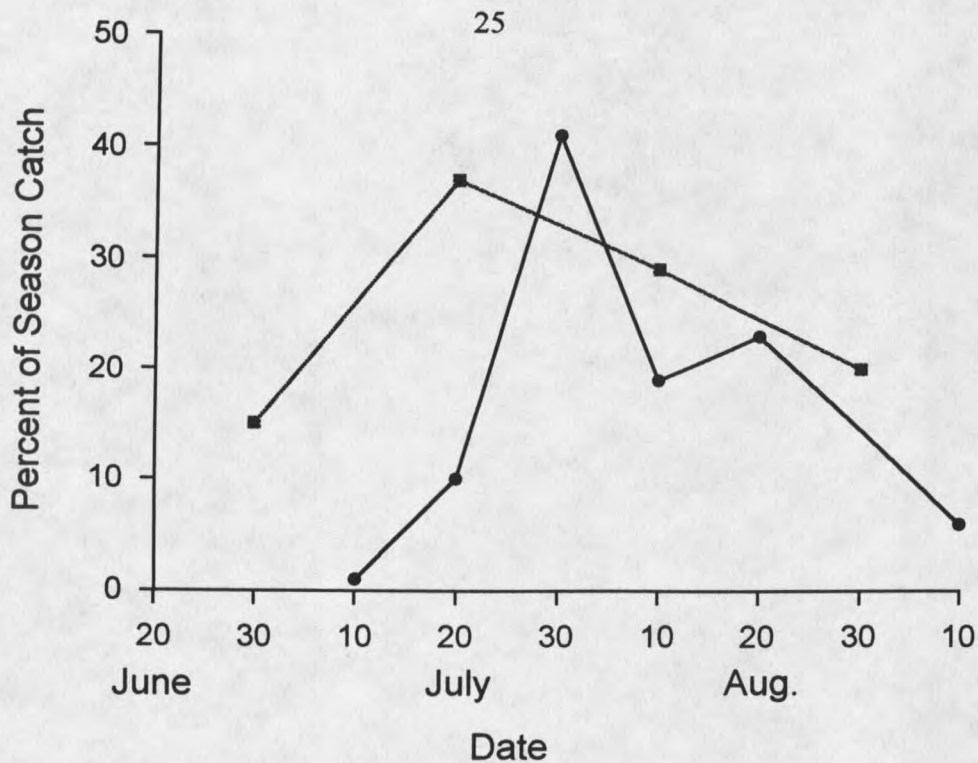


Figure 7. Seasonal occurrence of army cutworm moths at an alpine light trap (2150 m) located adjacent to a moth aggregation site in Glacier National Park, Montana, 1994 (circles) and 1995 (squares).

Hill, and Fergus counties of north-central Montana (Fig. 8). In Carbon county in south-central Montana (Fig. 2, Fig. 8), peak moth abundance occurred after the first week of September in 1993, but not until the first week of October in 1994 (Fig. 8).

Nutritional Value Of Moths

Cutworm moths showed a marked increase in wet mass, total moisture, total lipid, and gross energy, over the course of the summer. Upon arrival in the alpine of GNP, army cutworm moths weigh about 0.10 g each. When they leave the alpine to remigrate to the plains in late summer, they weigh about 0.16 g each, a 60% increase

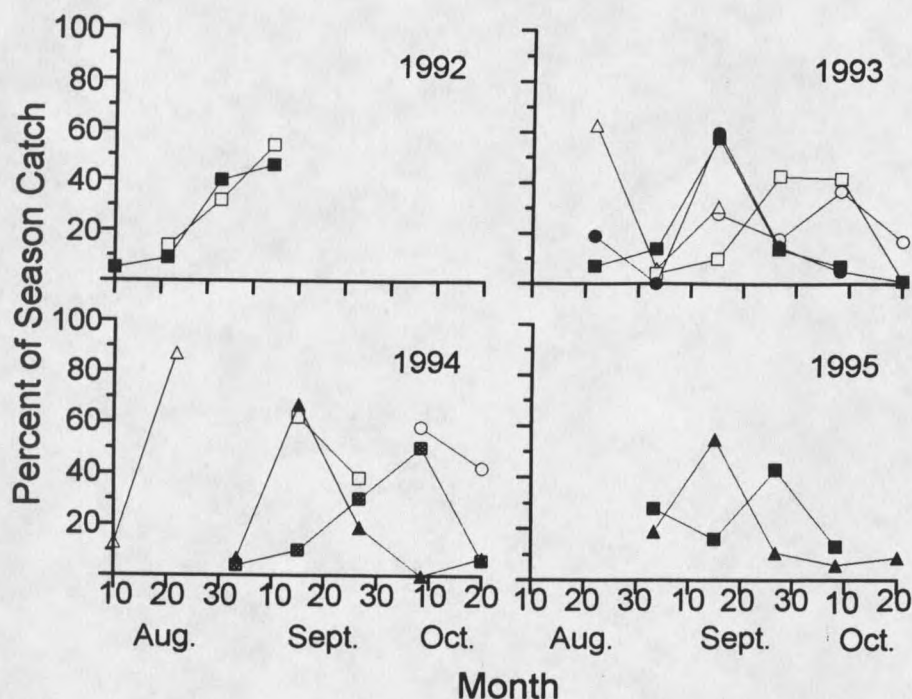


Figure 8. Seasonal occurrence of army cutworm moths at sex-attractant traps located adjacent to wheat fields in 6 counties in north-central and south-central Montana, 1992-1995. Pondera county, closed squares; Liberty county, closed triangles; Hill county, closed squares; Chouteau county, closed circle; Fergus county, open triangles, and Carbon county, open circles.

in body mass in 8 weeks (Fig. 9). There was a corresponding increase in total body moisture (Fig. 10). Total lipid (ether extract) was 40-55% in late June to mid-July and increased to about 70% by early September in 1994, and to 60% in 1995 (Fig. 11).

Gross energy content of moths was approximately 6 kcal/g in late June or early July and increased by one-third to about 8 kcal/g in early September in 1994 and 1995 (Fig. 12). In contrast, total nitrogen (crude protein), which was 35-40% in late June or early-July when the moths first arrived in the alpine, decreased to 25% in early September in 1994 and to less than 10% in 1995 (Fig. 13).

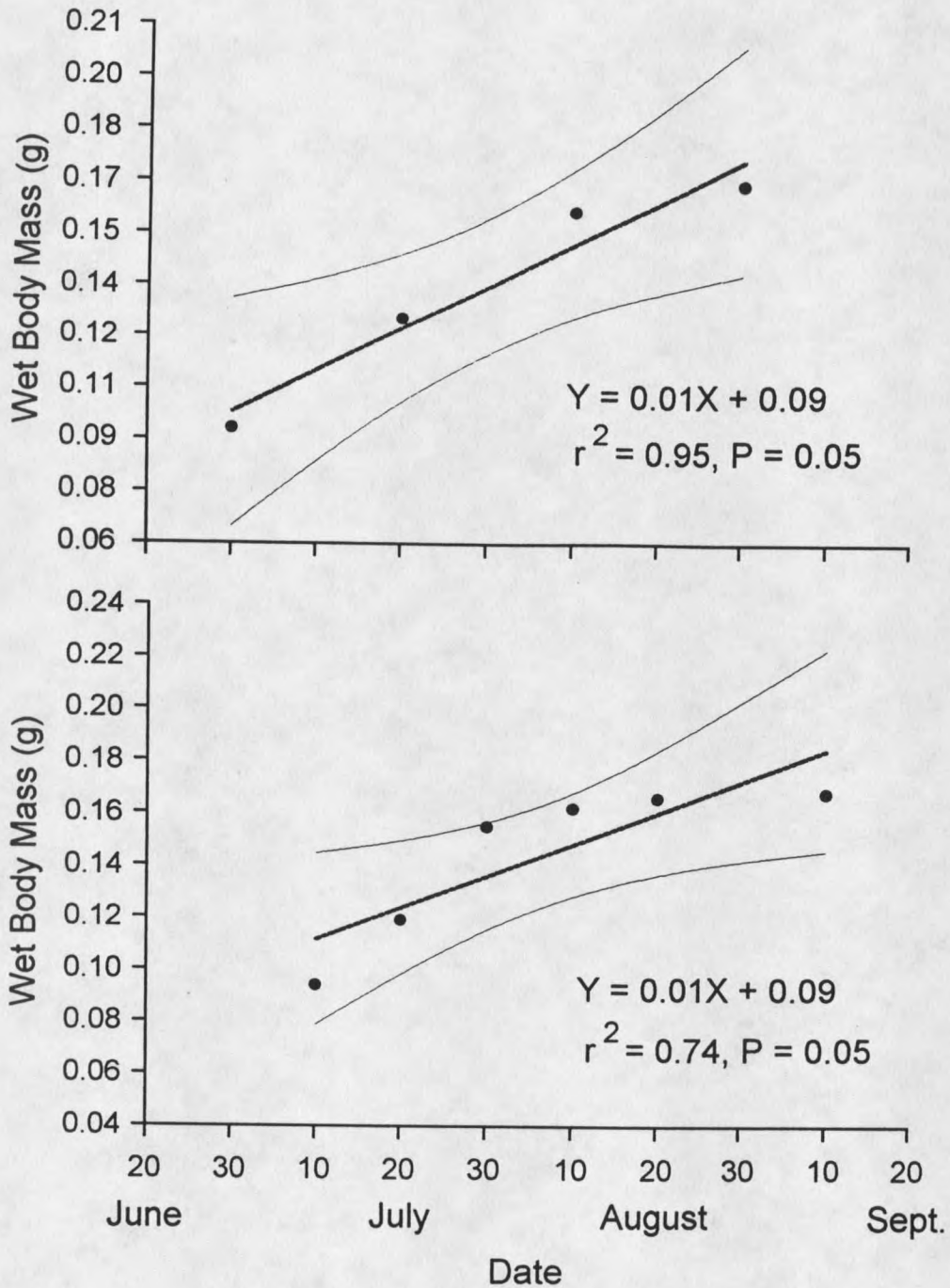


Figure 9. Wet mass of moths captured at an alpine light trap (2150 m) located adjacent to a moth aggregation site in Glacier National Park, Montana, 1994 (bottom), 1995 (top).

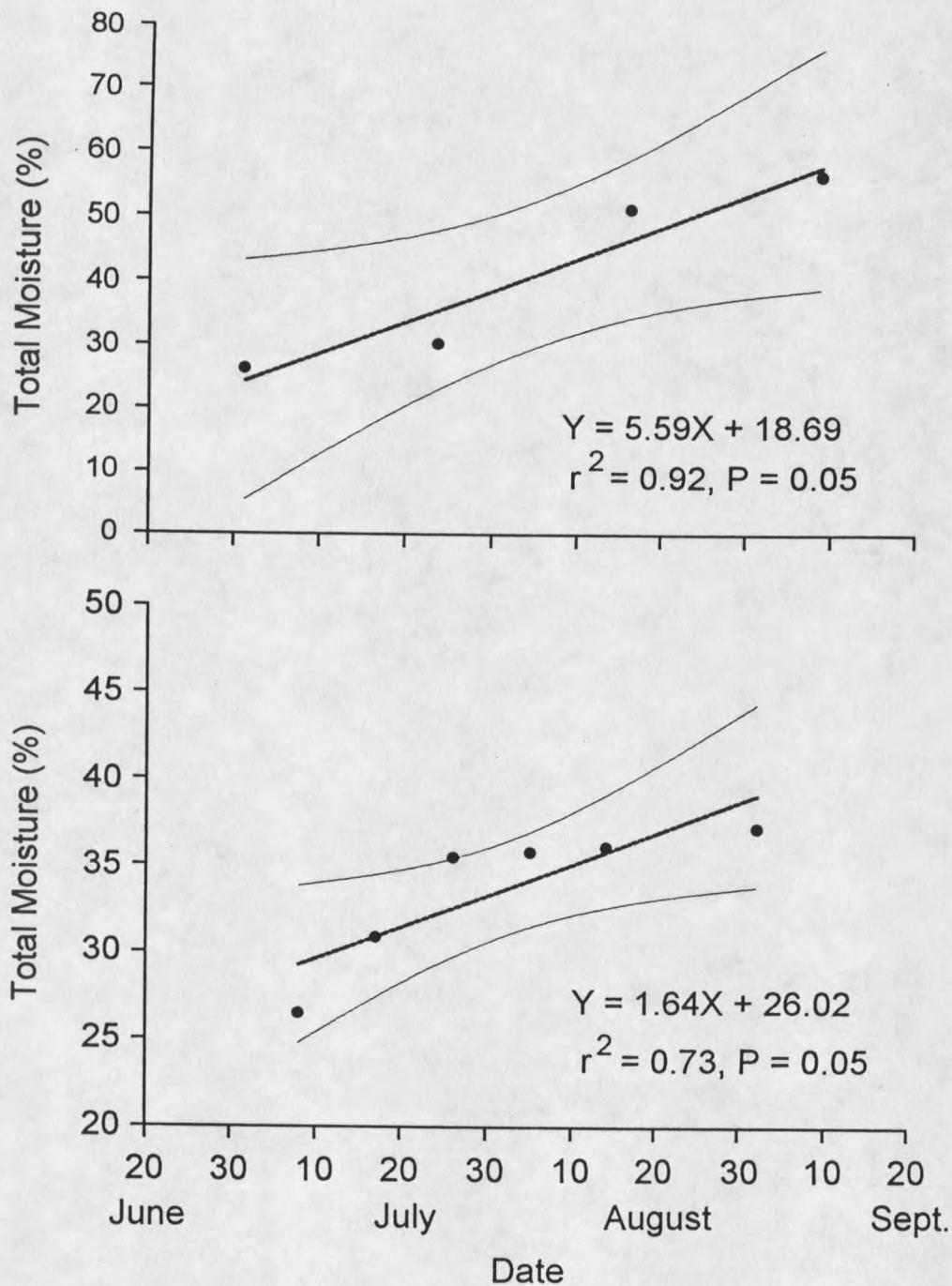


Figure 10. Total body moisture of moths captured at an alpine light trap (2150 m) located adjacent to a moth aggregation site in Glacier National Park, Montana, 1994 (bottom), 1995 (top).

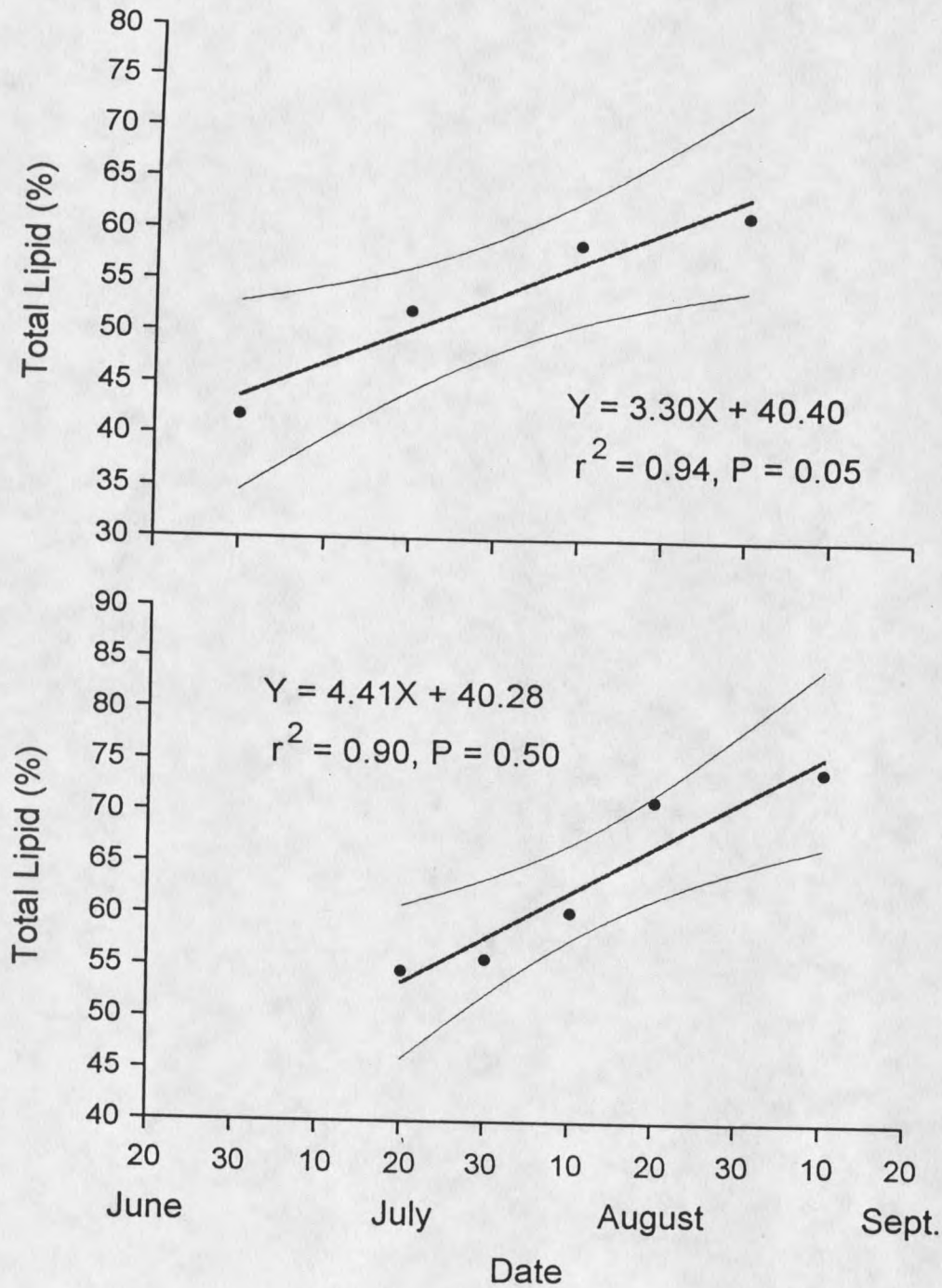


Figure 11. Total lipid (ether extract) of moths captured at an alpine light trap (2150 m) located adjacent to a moth aggregation site in Glacier National Park, Montana, 1994 (bottom), 1995 (top).

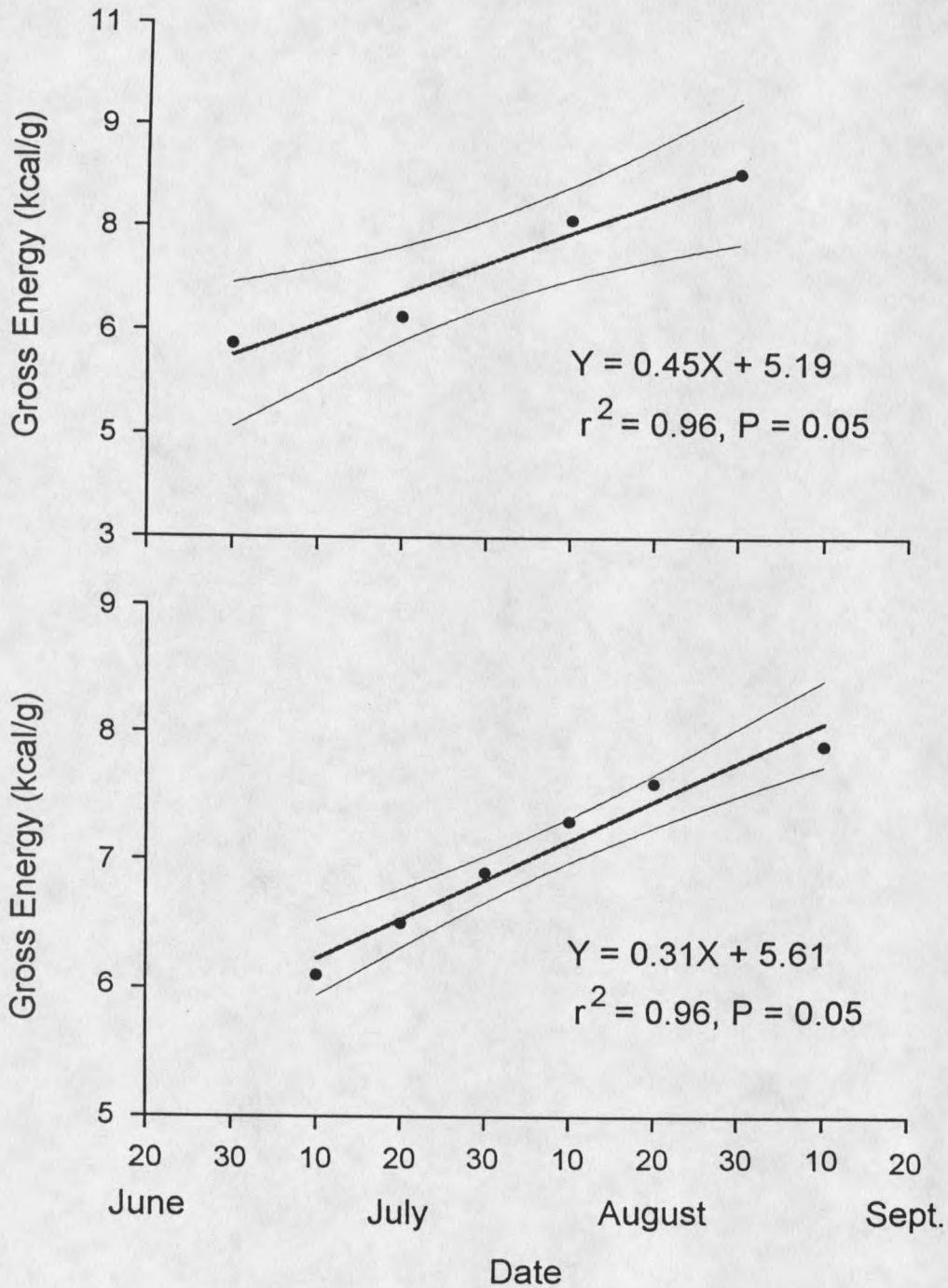


Figure 12. Gross energy content of moths captured at an alpine light trap (2150 m) located adjacent to a moth aggregation site in Glacier National Park, Montana, 1994 (bottom), 1995 (top).

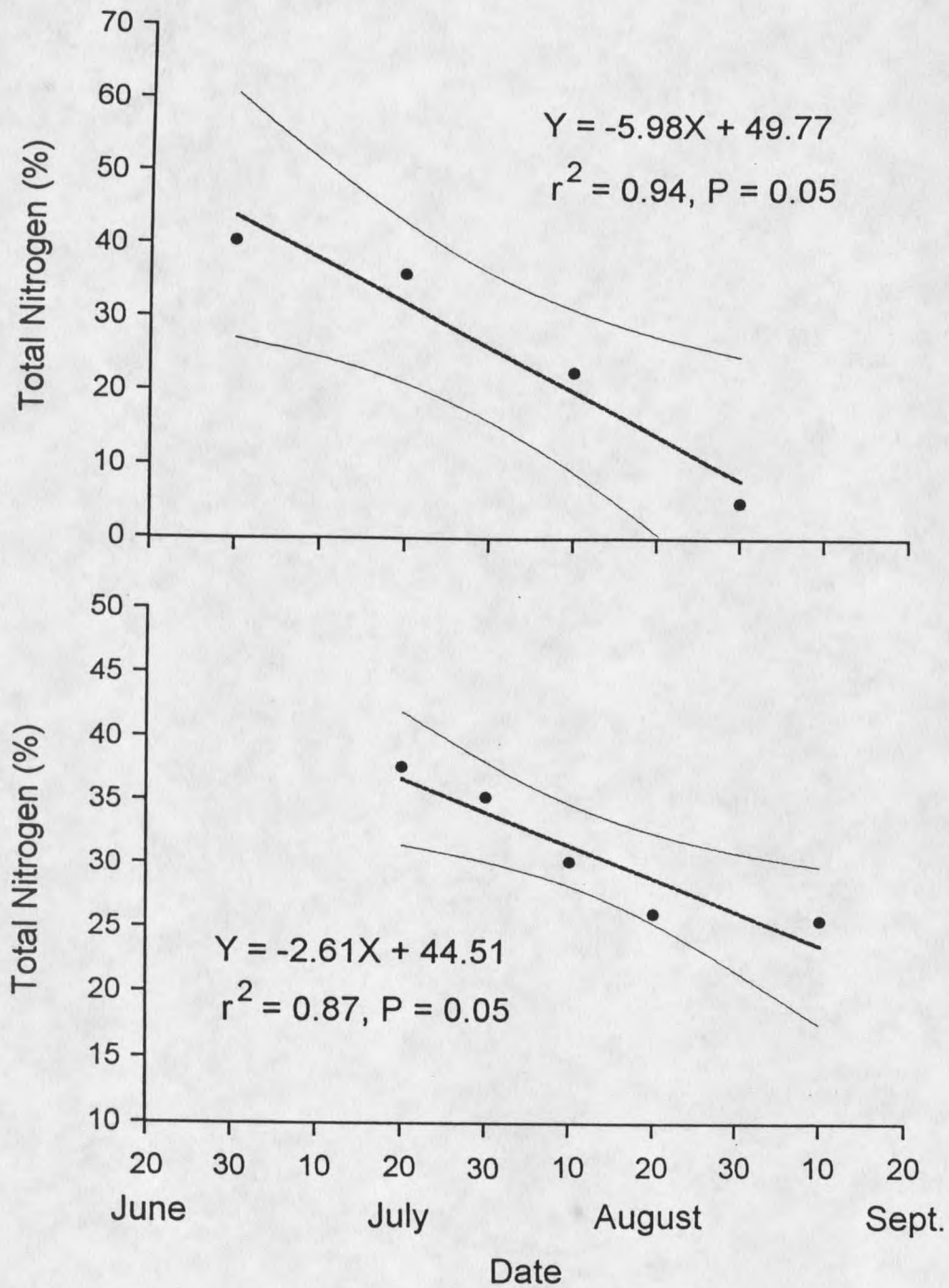


Figure 13. Total nitrogen (crude protein) of moths captured at an alpine light trap (2150 m) located adjacent to a moth aggregation site in Glacier National Park, Montana, 1994 (bottom), 1995 (top).

The energetic cost of migration was estimated by comparing the lipid content of pre- and postmigrants. The nutritional content of moths collected on the plains indicated a large decrease in body constituents compared to alpine collections. In Liberty county in 1994 total moisture was only about 6-8% (Table 5). Total moisture was much higher in Carbon county in 1994 and in Pondera, and Liberty counties in 1995 (Table 5). Total lipids also decreased dramatically. In Liberty and Carbon counties in 1994, total lipids ranged from 5 to 28 percent, being highest in early September and lowest in mid-October (Table 5). Concurrent with low lipid levels, gross energy content ranged from only 3-6 kcal/g in mid-September to early October in Liberty and Carbon counties in 1994 (Table 5).

I calculated the potential number of kcal a bear could ingest in a day while moth foraging by estimating the number of moths in a bear scat and multiplying by the number of times a bear defecated in a day. The mean number of moths in 24 bear scats examined was 3600. Based on observing 3 adult grizzly bears continuously for 3 days, a bear defecated about 11 times per day while foraging on moths. Hence, in years when cutworm moths are abundant (i.e., 1992), a grizzly bear can consume almost 40,000 moths per day, or about 2500 moths per hour. At 0.5 kcal per moth in mid- to late August, a grizzly bear while feeding extensively on army cutworm moths in the alpine of GNP, can consume up to 20,000 kcal per day.

Sizemore (1980) estimated the annual energy budget of a grizzly bear using theoretical energetic equations. A 115 kg bear requires approximately 960,000

Table 5. Chemical composition of army cutworm moths collected in 3 counties in Montana, 1994 - 1995. Numbers are percentages based on dry weight of moths.

Date	Liberty, Co., MT 1994				Carbon, Co., MT 1994				Liberty, Co., MT 1995				Pondera, Co., MT 1995			
	TM ^a	TN ^b	TL ^c	GE ^d	TM	TN	TL	GE	TM	TN	TL	GE	TM	TN	TL	GE
Sept. 1									47			5.9	42			6
10	6.4		28	3.4												
20	8.1		18	3.1	14	11	14	5	52	12	11	5.3	65	12	8.8	5.5
30	6.9			5.1	26	12	5.2	4.7								
Oct. 1																
10					20	13	6.1	5.2								

^aTM = Total moisture.

^bTN = Total nitrogen (crude protein).

^cTL = Total lipid (ether extract).

^dGE = Gross energy (kcal/g).

kcal/year. If a grizzly bear, consuming army cutworm moths in GNP, can consume 15,000 kcal/day for 30 days, it can consume 450,000 kcal, almost half of its annual energy budget.

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, then 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 cost of transport in 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 cost of transport, could travel $0.474 \text{ kcal}/0.0034 \text{ kcal/km} = 140 \text{ km}$.

Moth Density In A Talus Slope

Moth density varied several-fold among talus sites examined. Density of moths on and within the talus debris in 1992 was 14.3 moths/m² of surface area (SD = 17.2, $n = 16$), in 1994 it was 6.7 moths/m² of surface area (SD = 11.2, $n = 16$) and in 1995 it was 5.8 moths/m² of surface area (SD = 6.3, $n = 16$). Five areas selected for their especially high densities in 1992 had 111, 120, 132, 164, and 178 moths/m². I consider these conservative estimates. While digging into the talus to count moths, many moths escaped detection by crawling out of the area being censused.

Potential Climber Disturbance

Grizzly bears foraging at moth aggregation sites are sensitive to disturbance from climbers. Access routes to several summits take climbers near or through moth foraging areas. On 7 separate occasions I observed a total of 11 bears stop feeding and either leave the moth site (this happened in 6 instances) or temporarily discontinue feeding activities until the climbers left the area (this happened in 1 instance). The amount of time moving and exhibiting defensive behaviors dramatically increased when climbers were in the area, compared to when they were not (Fig. 14). I did not

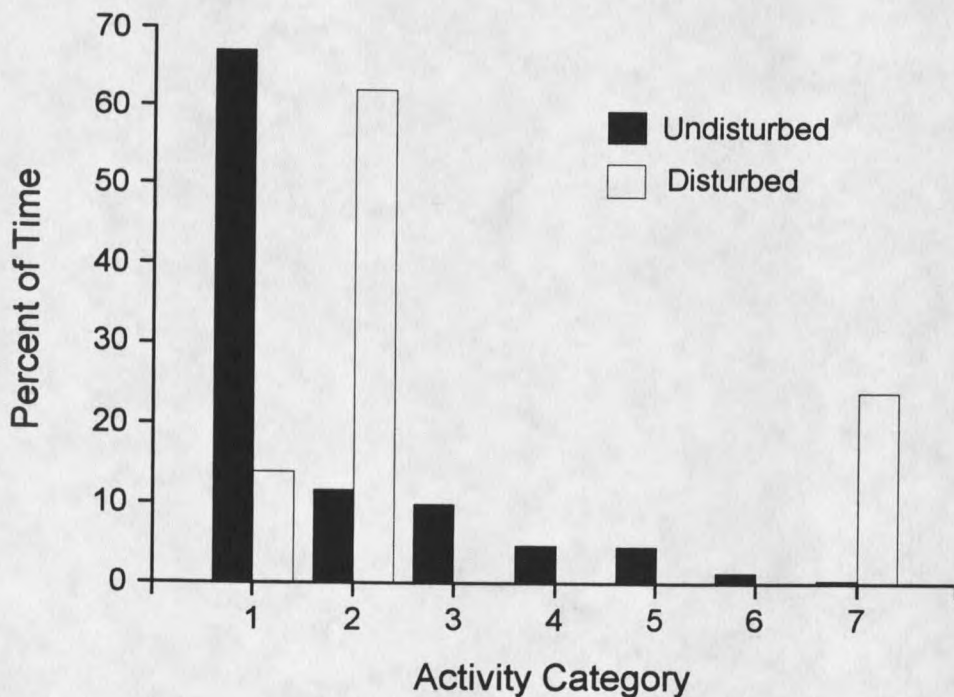


Figure 14. Activities of 18 adult grizzly bears foraging on a moth aggregation site undisturbed and disturbed by mountain climbers in Glacier National Park, Montana, 1992.

see any indication that the climbers knew the bears were nearby (i.e., within 100 - 200 m). Of the 9 bears I observed displaced from a moth site due to climber presence, none returned to the site that same day. All disturbance events occurred between 1100 and 1500.

Discussion

Grizzly Bear Use of Army Cutworm Moths

Over the past decade, a growing number of studies have documented extensive use of army cutworm moths by grizzly bears in the Rocky Mountain region of Montana. Klaver et al. (1986) observed 29 grizzly bears in July-September on McDonald Peak in the Mission Mountains, Montana, feeding on army cutworm moths. Eighteen of these bears were adult females with cubs. The Interagency Grizzly Bear Study Team first documented bears using moth aggregation sites in the Absaroka Mountains east of Yellowstone National Park, Wyoming in August of 1986. Since then, 14 moth site complexes, containing 27 moth sites, have been found (O'Brien and Lindzey 1994). In 1991 and 1992, 45% ($n = 107$) and 43% ($n = 102$), respectively, of all known bears in the Greater Yellowstone Ecosystem ($n = 236$) used moth sites (O'Brien and Lindzey 1994). Bears fed at these moth aggregation sites between 15 June and 15 September with peak use in mid-August (Mattson et al. 1991; French et al. 1994; O'Brien and Lindzey 1994). Of grizzly bears observed at 2 moth complexes in 1991 and 1992 in the Absaroka Mountains, females with cubs comprised 69% of the observations, with

lone adults (16.9%) and subadults (14.1%) making up the remainder (O'Brien and Lindzey 1994).

The proportions of age/sex classes I observed at moth aggregation sites in GNP differed from observations by Klaver et al. (1986) and Mattson et al. (1991) from moth sites in the Mission Mountains and the Absaroka Mountains, respectively. The frequencies of observation of adults versus females with young versus subadults were significantly different between my study and Mattson et al. (1991) ($G = 11.17$, $df = 2$, $P = 0.004$), and marginally different between my study and Klaver et al. (1986) ($G = 6.01$, $df = 2$, $P = 0.056$). The differences between GNP and the Mission Mountains, although marginal, are attributable to proportionately more observations of lone adults and fewer observations of females with cubs. The differences between GNP and the Absaroka Mountains are attributable to fewer observations of lone adults and more observations of subadults.

Mattson et al. (1991) found significantly fewer lone adults than females with young and subadults from moth aggregation sites in the Absaroka Mountains, and the Mission Mountains. They attributed the differences to proportionately more observations of lone adults and fewer of subadults. They hypothesized, as Klaver et al. (1986) did, that the more security-conscious or subordinate bears disproportionately used moth aggregation sites in the Mission Mountains, and that these sites afforded refuge from lone adults.

Stonorov and Stokes (1972) found similar diurnal foraging/behavioral activities at McNeil River Falls, Alaska. Dominant bears, usually male, controlled the limited number of fishing sites to the exclusion of all other bear cohorts. Each bear or family group waited its turn to fish. Once the choice fishing sites were relinquished, subordinate bears would then occupy these sites in order of their social position. Bunnell and Tait (1981) suggested that in the Ursidae, aggression by adult males is directed toward subadult males resulting in the eviction of the latter or their voluntary evacuation from the area. The social status of an animal may, therefore, affect its visitation frequency to moth aggregation sites.

Mattson et al. (1991) believed habitat differences between the Absaroka and Mission Mountains explained the differences in proportions of lone adult and subadult grizzly bears using moth aggregation sites in these 2 areas. They contend that because the Mission Mountains have an abundance of fleshy fruits in August and September, which they presumed were of greater or at least comparable quality relative to cutworm moths, fleshy fruits are likely exploited much more heavily by dominant lone adult bears than by subadult bears. In the Absaroka Mountains, fleshy fruits are scarce; these bears, therefore, are afforded fewer foraging options than bears in the Mission Mountains. Lone adult bears in the Absaroka Mountains, therefore, appear to rely more heavily on alpine moth aggregations than in the Mission Mountains.

Similarly, I found proportionately fewer lone adults and more subadults in GNP compared to the Absaroka Mountains. However, I found that cutworm moths

collected from alpine moth aggregations sites in GNP represented a high-quality food source for bears in August and early September. The gross energy content of moths collected in late August approached or exceeded 8.0 kcal/gm dry matter. This exceeds the gross energy content of other bear foods: blueberries (*Vaccinium corymbosum*) = 4.47 kcal/gm dry matter, Columbian ground squirrels (*Spermophilus columbianus*) = 5.28 kcal/gm dry matter, cutthroat trout (*Salmo clarkii*) = 5.71 kcal/gm dry matter, and mule deer (*Odocoileus hemionus*) = 7.32 kcal/gm dry matter (Prichard and Robbins 1990). If food quality alone is driving lone adult habitat selection, I would expect disproportionately more lone adults than subadults to utilize army cutworm moths in GNP than I actually observed.

Bear Activity Patterns

Grizzly bears principally spent their active time on a moth site foraging on moths. Based on 104 hours of observing 18 adult grizzly bears forage at 6 moth aggregation sites in 1992, grizzly bears foraged for moths in a bimodal pattern (Fig. 5). Activity studies that found black bears to be crepuscular attributed this pattern to their avoiding mid-day heat (Garshelis 1978) while still using daylight for foraging (Eubanks 1976). Activity levels for black bears in Great Smoky Mountains National Park were found to decline when temperatures exceeded 20 °C (Quigley et al. 1979). If bears observed in this study were responding strictly to temperature, I would expect to observe

increased or prolonged activity on cooler days. I detected no such relationship based on temperatures taken at 1 moth site in August and early September, 1995.

Foraging constraints imposed by the thermal characteristics of a talus slope may explain the timing of grizzly bear moth feeding. When I excavated moths in the cool of the morning, moths were located within 10 cm of the surface of the talus, but by the afternoon when temperatures on the surface are high, the moths are located greater than 20 cm deep within the rock debris where it is cooler. Grizzly bears fed on moths during the cooler parts of the day, morning and evening. Bears were usually already feeding on moths when I arrived at my observation posts at 0600. They fed until about noon then were inactive on sites until about 1600. At this time, they resumed feeding and continued until they left the area later in the evening.

Grizzly bears possibly foraged on moths in the morning and evening hours because the moths were distributed near the surface of the talus and easily captured. When moths were less available to bears, as during the heat of the day, the energetic costs associated with digging for moths deep in the talus, probably exceeded energetic yield.

Nutritional Value of Moths

Knowledge of the body composition and relative energy values of army cutworm moths is important in order to understand the nutritional implications, ecology, and foraging behavior of grizzly bears while they are utilizing moth aggregation sites.

Army cutworm moths showed a linear seasonal difference in total nitrogen, total lipid, and gross energy. Similarly, army cutworm moths showed an overall increase in percent abdominal lipid over the summer months on Pennsylvania Mountain, CO. (Kendall 1981). Mean June abdominal lipid values for male and female cutworms captured in 1979 and 1980 were 38% and 46%, respectively. Mean July abdominal lipid values for male and female moths captured in 1978-1980 were 72%, 51%, and 64%, respectively. O'Brien and Lindzey (1994) also found a seasonal increase in whole-body lipids in army cutworm moths captured in the alpine of the Absaroka Mountains. Mean August whole-body lipids for male and female moths in 1991 were 63% and 69%, respectively. Mean September lipids for male and female moths were 60.5% and 72%, respectively. In 1992, mean July lipids for male and female moths were, 56% and 59% respectively. Mean August lipids for male and female moths were 61% and 68%, respectively.

The high lipid levels towards late summer may indicate preparation for remigration back to the plains. Flight is one of the most energetically demanding activities, and the primary flight fuel in lepidopterans is lipid (Weis-Fogh 1952; Gilbert 1967; Mason et al. 1990). The low 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 *Danaus plexippus* (Beall 1948), *Agrotis infusa* (Common 1954), *Pseudoplusia includens* (Mason et al. 1989), and *P. scabra* (Mason et al. 1990).

Where the army cutworm moths that summer in the alpine of GNP originate is unknown, but my capture data demonstrate the timing of migration and remigration. I began capturing army cutworm moths in alpine-located light traps in late June. Peak moth abundance occurs in mid- or late July. The moths leave the alpine by late August or early September. Cutworm moths appear in sex-attractant traps on the plains of north-central Montana in late August. Most of the captures in these areas occurs in late September and early October. Virtually no moths were trapped in late October.

Army cutworm moths remigrate from the alpine of GNP with a 60-75% total body lipid content. They arrive in north-central Montana with lipid reserves depleted down to 30% or less. By determining experimentally the rate a moth metabolizes lipids during flight, one could potentially estimate remigration distances.

Based upon examination of bear scats taken from moth aggregation sites in GNP, cutworm moths appear to be highly digestible; essentially all moth parts are digested except for their exoskeletons. Army cutworm moths, therefore, appear to provide a concentrated (e.g., moths are about 8.0 kcal/gm in August), readily available, and highly digestible source of energy during summer and early autumn.

Nutrition has been implicated as an important factor which may influence both reproduction and mortality in black bear populations. Rogers (1976, 1977) and Jonkel and Cowan (1971) found that reproductive rates declined when berry crops were poor in Minnesota and Montana, respectively. Age of sexual maturity, breeding intervals, and litter size were all altered by nutritional factors. Additionally, delayed hibernation

and even failure to hibernate occurred when Russian brown bears were malnourished in autumn due to nut and berry failures (Pavlov and Zhdanov 1972, Ustinov 1972).

Jenness (1985) noted that, "milk composition was greatly influenced by diet and early spring condition of female bears depends upon, to a large extent, fall nutrition." The access of abundant summer/autumn foods, such as moths, may influence the quality and quantity of milk produced by a lactating female resulting in better health and subsequent increased survival of her offspring.

Migration potential

Koerwitz and Pruess (1964) demonstrated that army cutworm moths are physically capable of making migratory flights from the Great Plains to the Rocky Mountains by using a flight mill to determine flight range. By feeding the moths in their study a honey-water solution prior to each flight, Koerwitz and Pruess (1964) showed that army cutworm moths could fly up to 300 km in about 65 hours. 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, moths unfed and newly emerged made only short single flights of less than 8 km before exhaustion (Koerwitz and Pruess 1964).

Army cutworm moths may be using different strategies to fuel their spring and fall migrations. The moths used in the study by Koerwitz and Pruess (1964) were only 5-15% whole body lipid in the spring, excluding 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 (i.e., a pay-as-you-go strategy) and lipids during the fall migration after they have had opportunity to accumulate adequate lipid levels (i.e., a living-off-of-savings strategy).

I calculated that army cutworm moths that remigrate from the alpine of GNP in late summer have enough energy stored as lipid to fly approximately 145 km. If army cutworm moths are migrating several hundred km from the Great Plains or from the midwestern States in the spring, the migratory potential of 145 km falls short of the actual flight distance. Several factors may explain this inconsistency. 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 fall in GNP, strong western and northwestern winds are common. It is plausible that remigrating cutworm moths utilize these tail winds to reduce cost of transport and save energy stores. 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, insufficient data about ambient winds during remigration and of the ways in which cutworm moths adjust their flight path in

response to winds limit our ability to utilize these factors in estimating migratory potential.

Moth Use Of Talus Slopes

Army cutworm moths occupy the cracks and crevasses of talus slopes for possibly 2 reasons. First, the rock provides protection from avian predators, although birds still eat them. Ravens (*Corvus corax*) light near foraging bears and pick off stray moths that take flight when they are uncovered by the bears' activities. I have also observed Clark's nutcrackers (*Nucifraga columbiana*) and gray-crowned rosy finches (*Leucosticte tephrocotis*) eating army cutworms on moth sites.

Secondly, moths possibly use talus slopes for thermoregulation. There is a steep thermal gradient within the talus debris, particularly at mid-day (Fig. 2). It is 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 cm into the talus the temperature is 10 °C cooler. At 20 cm deep, the temperature is 14 °C cooler than the surface. Army cutworm moths appear to choose the thermal environment within the talus most suitable for them at any particular time of day: near the surface in the mornings, deep within the talus in the afternoon, back to the surface as temperatures cool towards evening.

An Energetic Mosaic Foraging Hypothesis

Hamer (1985) noted five factors that may influence grizzly bear movements and choice of habitat: learned family traditions, reproductive processes, defense or exploration of home ranges, use of cover, and/or resource partitioning between sex and age classes. Given the dominant role of feeding in the activities of grizzly bears (Herrero 1985, Hamilton and Bunnell 1986), landscape-level habitat and home range use patterns presumably are coarse reflections of animal foraging behavior in the absence of disturbance. Several field studies of grizzly bear foraging strategies, including proximate analysis of selected food items, appear in the literature (Mealey 1980, Hamer et al. 1977, Graham 1978, Hamer et al. 1979, Lloyd 1979, Reinecke and Owen 1980, Sizemore 1980, Hamilton and Bunnell 1986). However, the role of forage quality and availability in determining habitat selection by grizzly bears and how these phenomena relate to grizzly bear fitness is less well understood.

The digestive system of a grizzly bear is essentially that of a carnivore (although elongated) with herbivorous adaptations of modified dentition (e.g., relatively long, flat molars with grinding surfaces) and lengthened foreclaws (David 1964, Herrero 1985). Grizzly bears do not have a caecum, and Rogers (1976) reports that bear stomach fluid acidities are too low for the propagation and maintenance of microflora and microfauna necessary for cellulose digestion. Subsequently, a grizzly bear has limited capability to digest coarse (that is, high dietary fiber) forage efficiently (Bunnell and Hamilton 1983, Grizzly Bear Compendium 1987). This digestive inefficiency,

combined with preparation for self-maintenance during winter dormancy and spring hypophagia, has led to speculation that grizzly bear habitat selection is related to the quantity and quality of available forage (Lloyd 1979, Mealey 1980, Sizemore 1980, Stelmock 1981, Craighead et al. 1982, Hamer and Herrero 1987, Hamer 1985, Hamilton and Bunnell 1986).

The dramatic seasonal shifts in the diet of grizzly bears are well documented (Herrero 1985, Hamilton and Bunnell 1986). Optimal foraging theory assumes that animals increase their fitness by maximizing their net rate of energy intake (Schoener 1971, Werner and Hall 1974, Charnov 1976a, 1976b, Pyke et al. 1977). The seasonal dietary shifts exemplified by grizzly bears may result from attempts to maximize their net rate of energy intake by selecting highly digestible forage (Bunnell and Hamilton 1983, Hamilton and Bunnell 1986). Additionally, because all components of a grizzly bear's reproductive rate (litter size, breeding interval, and age at first reproduction) and survival are thought to be under some nutritional control (Bunnell and Tait 1981), some optimality in foraging behavior is expected (Bunnell and Hamilton 1983).

For a grizzly bear, meeting nutritional requirements is a complex and highly variable interaction of time-space events (Mealey 1980, Hamer and Herrero 1987, Hamilton and Bunnell 1986, Bunnell and Hamilton 1983, U.S. Fish and Wildlife Service 1993). Generally, upon emergence from the den in March through May, grizzlies move to lower elevations to find immature, succulent, high protein, highly digestible forbs. Drainage bottoms and avalanche chutes with southern exposures are

particularly productive in the early spring of the year. Here grizzlies find the shoots, leaves, and stems of most forbs succulent, easily digestible, and high in nutrients compared to later growth stages when flowering, fruiting, or dormancy has occurred (Herrero 1985). Ungulate winter ranges also provide food resource possibilities (Bunnell and Hamilton 1983).

Through late spring and early summer grizzly bears follow the plant phenology into higher elevations where plant growth is accelerated creating a greater percentage of protein in plant tissue compared to lower elevation sites (Johnston et al. 1968). Foraging bears can also move to north-facing aspects where moisture provides a prolonged growing season and maintains succulence and nutrient levels in forage species (Mealey 1980, Herrero 1985). In Alaska, coastal brown bears have been observed to spend up to six weeks feeding on emerging sedges as the snowpack gradually receded up a mountain slope (Atwell et al. 1980). The plants eaten by bears will obviously vary from region to region, but the principle of foraging on the early growth stages of plants is a general rule (Herrero 1985). In late summer and fall, most grizzly bear populations exhibit a transition to fruit and nut resources and are the primary foods used for weight gain in preparation for denning. Some populations utilize aggregations of army cutworm moths to supplement or, in some individuals, replace fruits and nuts.

Because of the biotic and abiotic complexity found in grizzly bear habitat grizzly bears forage upon food items that exhibit an exceedingly complex chemical spectrum.

The chemical composition of a species of plant is highly variable depending on any one or combination of the following: plant type, plant part, phenology, climate, season, weather, soil type and fertility, soil moisture, leaf stem ratio, physiological and morphological characteristics, and others (Kilcher 1981). That selected grizzly bear foods show a similar declining nutrient composition and increasing plant fiber content with advancing development is well documented (Kilcher 1981, Hamer and Herrero 1986). A grizzly bear's movement patterns are possibly investigative forays to find locations where forage species are immature, highly nutritious, and easily digested.

Since several animal species have been demonstrated to increase their fitness by maximizing their rates of net energy gain (e.g., Krebs et al. 1974, Huey and Slatkin 1976, Stenseth 1978) and grizzly bear litter size, breeding interval, age at first reproduction, and survival are influenced by diet, I propose that selection pressures operating on grizzly bears have encouraged the means to enhance energy intake and that grizzly bears select forage species that are highly digestible and nutritious. Little data are available, however, on the relationships between forage quantity and quality and the seasonal movements and habitat use by grizzly bears.

Army cutworm moths appeared to be distributed nonuniformly on a talus slope. The mean density of moths was approximately 6 to 14 moths/m². Much larger densities occurred, however. In 1992, a minimum of 178 moths/m² were counted. This represents an energy distribution of at least 90 kcal/m². Most of these high-density moth areas were associated with deep (> 1 m) talus debris. Given the

nonuniform distribution of moths on a talus slope, it is useful to view a moth aggregation site as an energetic mosaic: high energy patches interspersed within a much larger low energy matrix. Because the energy distribution on a talus slope can be mapped and grizzly bear foraging behavior can be easily observed and mapped, grizzly bear use of moth aggregation sites may provide an adequate model to empirically test the relationships between forage quantity and quality and the seasonal movements and habitat use by grizzly bears.

It should be noted that using total digestible energy, protein content, or some other measure of grizzly bear forage quality is potentially misleading and could possibly lead to a misunderstanding of grizzly bear foraging strategies and habitat use. Foods may be chosen on the basis of vitamin or mineral content or other criteria (Hamer and Herrero 1983, Hamilton and Bunnell 1986). Presence of protective or defensive agents could cause avoidance of certain food items by grizzlies (Robbins 1983) as well. In considering the factors that influence grizzly bear selection of habitat, one would do well to heed the warning given by Hirnstein (1984): "The temptation to fall back on common sense and conclude that animals are adaptive, i.e., doing what profits them most, had best be resisted, for adaptation is at best a question, not an answer."

Disturbance Potential

Human influence on the selection of food and feeding sites in a protected area such as GNP, primarily involves supplementation (and subsequent attraction) and

disturbance (and subsequent loss of feeding opportunities). Glacier National Park is a favorite destination for mountaineers. About one third of the Park's 410,000 ha occurs above timberline. Subsequently, many access routes to these alpine vistas take climbers near or through moth aggregation sites. This potential for human disturbance of foraging grizzly bears concerns managers. Although difficult to quantify, human disturbance may reduce food intake through interruption of foraging bouts or by displacement from feeding areas, and may increase energy expenditure from additional time moving. Reduced food intake and increased energy expenditure could potentially affect the ability of bears to acquire nutrient reserves for successful reproduction. Furthermore, nutrient reserves acquired during the late summer and early autumn may influence winter survival.

Bear sensitivity to human presence has been documented in several areas. Brown bears are known to avoid feeding areas when more than 4 people were present at McNeil River Falls, Alaska (Stonorov and Stokes 1972). Given the history of human intrusiveness in this area, these bears may be more habituated to humans and consequently should display less of a sensitivity to human presence than grizzly bears feeding on moths in GNP. Even at distances greater than 1000 m, bears may be aware of human presence due to wind currents and noise resulting in a disruption of normal feeding activities.

Because of potential conflicts between bears and humans, Klaver et al. (1986) recommended closure of McDonald Peak in the Missions Mountains, Montana,

commensurate with bear arrival (usually late July) and departure (1 October). Closure began in 1981 and remains in effect to date. The goal of this action was to reduce human-bear interactions and conflicts, bear habituation, disturbance of females with cubs, and to prevent teaching cubs human habituation tendencies (Klaver et al. 1986). The plan received strong public support, in part due to an effective public relations and education program.

The importance of climber disturbance can be expressed as amount of lost energy due to interrupted feeding time. If a grizzly bear can consume 40,000 moths per day, or 2500 moths for every hour of feeding time, every minute a bear does not eat due to disturbance costs the bear 42 moths. At 0.5 kcal per moth in late August, disturbance costs the bear 21 kcal per minute, not counting the energy expended in defensive behaviors and leaving the moth site.

Management Implications

Grizzly bear habitat loss and population declines occurring concurrently with increasing human populations have been well documented in Europe and North America (U.S. Fish and Wildlife Service 1993, Roben 1980, Cowan 1972, Mysterud 1980, Buchalczyk 1980, Markov 1980, Roth 1976, Elgmork 1978, Grachev 1976, Kaal 1976, Vereschagin 1976, Pearson 1975, Curry-Lindahl 1972, Stebler 1972, Zunino and Herrero 1971, Guilday 1968, Buss 1956, and Storer and Trevis 1955). Human activities that occur within grizzly bear range have and will continue to have

effects, however subtle, on grizzly bears (Aune and Kasworm 1989). The recommendations included here are suggested ways to ensure that grizzly bears continue to have access to moth sites and that they can feed on these sites uninterrupted by humans.

If grizzly bears in the Northern Continental Divide Ecosystem in general and Glacier National Park in particular are to survive in the long term, their critical biological needs and important seasonal foraging areas must be identified and given high management priority. High elevation army cutworm moth aggregation sites may prove to be a natural food that is important in maintaining grizzly bears in Glacier National Park and careful management of these sites could therefore be critical for their conservation.

Although present rates of disturbance of grizzly bears on moth sites are probably low, increased human activity could affect the energetic budgets of foraging bears. Establishing controlled-human-use buffer zones around moth sites used by bears, determining alternate climbing routes for mountain peaks with moth sites on them, and establishing minimum flight elevation regulations for aircraft would not only reduce the chances for bear-human conflicts but would also decrease human disturbance on foraging grizzly bears.

A geographical information system was used to obtain a Park-wide perspective of potential moth site locations. Using elevation (2131-3114 m), slope (21-54°), and aspect (0-86°, 165-360° (East = 0°, North = 90°)) of the 9 moth study sites, I

determined other locations in the Park that have similar geographical and geological characteristics. According to my model, 10.5% of Glacier Park (about 43,000 ha) is potential army cutworm moth habitat (Fig. 15). Whether these areas are occupied by moths or if grizzly bears are feeding at these sites is unknown.

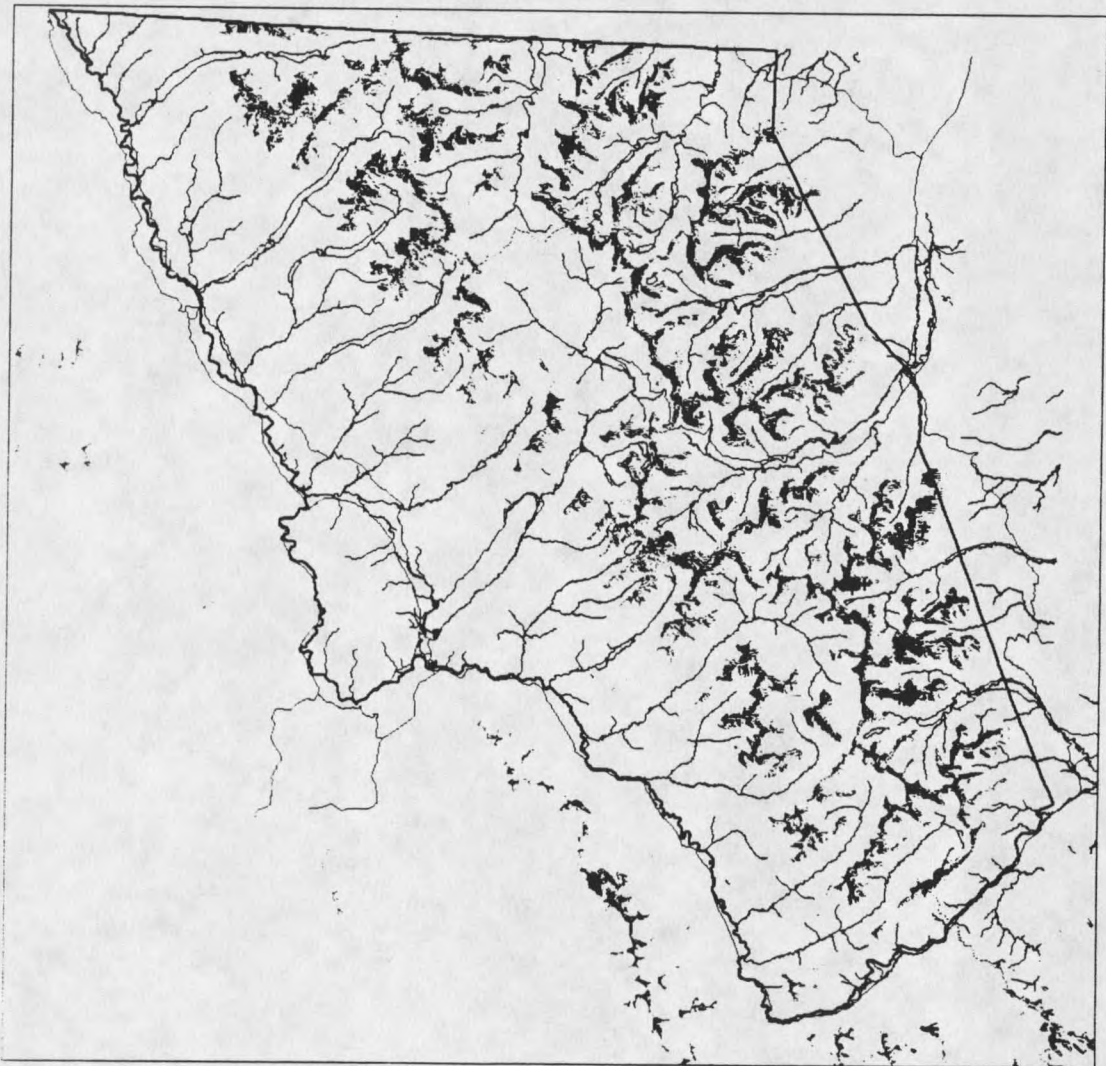


Figure 15. Distribution of potential moth aggregation sites in Glacier National Park, Montana.

PART B

REPRODUCTIVE CHARACTERISTICS OF THE MALE GRIZZLY BEAR
IN THE CONTINENTAL UNITED STATESIntroduction

Bears in northern temperate environments have a well-defined breeding season extending from May until early July. During the breeding season, testicular weights are higher than any other time of year. By September, testicles regress in size and by late September azoospermia occurs, although spermatozoa may be present in the epididymides (Erickson et al. 1964, 1968; Pearson 1975; Horan et al. 1993; Garshelis and Hellgren 1994). Testicular regression continues throughout the non-breeding season. Although the pattern or extent of regression differs among individual bears, by 1 October, the diameter of the seminiferous tubules is markedly decreased (Erickson et al. 1964, 1968; Pearson 1975; McMillin et al. 1976; Reynolds and Beecham 1980; Tsubota and Kanagawa 1989). By mid- to late October or early November, testicular regression is nearly complete; by mid-November the testicles are infiltrated by adipose tissue and loose, fibrous, connective tissue (Erickson et al. 1964, 1968; Pearson 1975). The tubules at this time are small and show no lumen, and the germinal epithelium consists only of Sertoli cells (Erickson et al. 1964, 1968).

Testicular weights in the early winter months are the lowest found in the mature bear throughout the year (Erickson et al. 1964, 1968; Pearson 1975).

Testicular recrudescence, which is well underway before emergence from winter denning (Erickson et al. 1964, Palmer et al. 1988, Garshelis and Hellgren 1994), generally involves seminiferous tubule enlargement and increased Leydig cell activity (Erickson et al. 1964, 1968; Pearson 1975). Active Leydig cell development and spermatogenesis, with the presence of spermatozoa in the epididymides, have been noted in bears killed in late May and early June to the middle or end of July (Erickson et al. 1964). Fully formed spermatozoa are present in seminiferous tubules and epididymides at least 1 month before and several months after the seasonal period of estrus in females in the European brown bear (*U. a. arctos*, Dittrich and Kronberger 1963), American black bear (Erickson et al. 1964), Alaskan brown bear (*U. a. middendorffi*, Erickson et al. 1968), grizzly bear (Pearson 1975), and the Hokkaido brown bear (*U. a. yezoensis*, Tsubota and Kanagawa 1989).

Although we have a general understanding of male brown bear (*U. a. spp.*) gonadal activity, most of our knowledge regarding the breeding activity of male brown bears is based on empirical observations. Few studies have characterized male brown bear reproductive biology, including testicular growth and spermatogenesis. Currently, no data are available for testicular growth and age of sexual maturity of grizzly bears in the continental United States.

Nearly all grizzly bears killed in the continental United States are necropsied at the Montana Department of Fish, Wildlife and Parks (MDFWP) Wildlife Laboratory in Bozeman, Montana. Due to the lack of information on male grizzly bear reproductive physiology and the fortuitous, although limited, availability of male reproductive tracts, I sought to: (1) evaluate testicular growth and seminiferous tubule development in grizzly bears ≤ 15 years of age, and (2) estimate age of sexual maturity in male grizzly bears from Montana and Wyoming. Although my conclusions are limited by small sample sizes, I present the only information available on testicular histology of male grizzly bears in the continental United States.

Methods

Testicles from 20 male grizzly bears were collected from bears killed by Federal and State wildlife personnel or hunters in Montana and Wyoming from 31 May 1978 to 27 August 1992. Age of each bear was determined by counting the cementum annuli of extracted premolars (Willey 1974; Coy and Garshelis 1992). As testicle collections were fortuitous, it was not possible to obtain specimens for all ages and seasons.

Usually within a few hours after death, the testicles of each bear were removed from the scrotum, dissected free of the tunica vaginalis, fixed in neutral-buffered formalin for several days, then stored in either 10% formalin or 70% ethanol at the MDFWP Wildlife Laboratory for ≤ 10 years. Tissue shrinkage and suboptimal staining

are known to occur by prolonged storage in fixative (Gale Callis, Dep. Vet. and Molecular Biol., Mont. State Univ., Bozeman, pers. commun., 1996). No corrections for shrinkage were made on my data.

Each testicle was weighed without the epididymis to the nearest 0.001 g using a Mettler PJ 300 digital balance. Testicle length and diameter were measured without the epididymis with vernier calipers to the nearest 0.1 cm. Using a dial scale, body mass was determined to the nearest pound and converted to kg; body length was measured with a tape to the nearest inch and converted to cm.

One of the 2 testicles from each bear was selected (right and left side were unknown) and cut transversely into 3 approximately equal sections that represented the top, middle, and bottom. Two 3-mm³ blocks were cut from each section (6 blocks of tissue/testicle), dehydrated in ethanol, and embedded in paraffin. Five sections (5 μ m thick) were cut from each block of embedded tissue at 3 locations within the block (i.e., front, middle, and back) and placed on separate glass microscope slides. Within each block, the 5 sections from each location within each block were separated by 150 μ m of tissue. Sections were removed from the paraffin and stained with Shandon hematoxylin 1 and eosin Y.

Three of the 5 sections from each location within each block (front, middle, and back) were chosen randomly and the diameters of seminiferous tubules were measured using a Zeiss 20 light microscope (100x) and an image analyzer (AUSKey 2.0, Animal Ultrasound Services, Inc., Ithaca, N.Y.). Tubular diameters were estimated by taking

the mean of 3 linear measurements at different axes that intersected at the center of the tubule. This procedure was repeated for each slide from each block taken from the top, middle, and bottom of each testicle. This represented 18 slides from each testicle with 30 seminiferous tubule diameters measured/slide.

Seminiferous tubules from each grizzly bear were examined visually under a Zeiss 20 light microscope (400x) for the presence of fully-formed spermatozoa. A bear was considered sexually mature if there were spermatozoa in the lumen of the seminiferous tubules.

To test whether seminiferous tubule diameter differed between the top, middle, and bottom of each testicle sampled, data for seminiferous tubule diameters were analyzed by analysis of variance for a split-split plot design using the General Linear Models (GLM) procedure of SAS (SAS 1987). Variables in the model included: part of testicle (top, middle, and bottom), block (2 blocks, 3-mm³) and slide (front, middle, and back), and all interactions. The error term for testing part of testicle was block within testicle and the error term for testing block was slide within block. Pearson correlation coefficients were calculated between age, body mass, body length and selected testicular traits in all animals using SAS. I used least-squares linear regression analysis to investigate the relationship between age and mean testicle mass for each bear. The effects of age on seminiferous tubule diameters were examined by fitting a nonlinear regression model to these data using the PROC NLIN procedure of SAS (1987). The proportion of grizzly bears 4.5 years old that lacked fully-formed

spermatozoa found in the lumen of seminiferous tubules and ≥ 5.5 years old that had fully-formed spermatozoa were analyzed using contingency chi-square. Testicular volume was estimated using the formula for a prolate spheroid (Beyer 1976). Data for testicle mass and volume, and mean seminiferous tubule diameter were examined by an analysis of variance using the GLM procedure (SAS 1987). The model included age class and date of kill. Means were compared using the LSD procedure (SAS 1987). Data for mature bears were grouped by season (the breeding season [May through mid-July] and the nonbreeding season [mid-July through November]) and analyzed using a *t*-test.

Results

There were no effects ($P > 0.10$) of blocks and sections, and there were no interactions ($P > 0.10$) of these variables among the other independent variables. Therefore, data for seminiferous tubule diameters were pooled to yield a single estimate for each bear (Table 6).

Age, body mass, and body length were correlated positively ($P < 0.01$) with testicle mass ($r = 0.76, 0.62,$ and $0.69,$ respectively), testicle length ($r = 0.70, 0.65,$ and $0.74,$ respectively), testicle diameter ($r = 0.69, 0.68,$ and $0.77,$ respectively), and mean seminiferous tubule diameter ($r = 0.60, 0.54,$ and $0.62,$ respectively).

Table 6. Age (yr), date killed, and testicular characteristics of 20 male grizzly bears from Montana and Wyoming, 1978-1992.

Age (yr)	Date killed ^a (M-D)	Testicle mass ^b (g)		Testicle length (cm)		Testicle diameter (cm)		Mean STD ^c (um)
		A	B	A	B	A	B	
1.5	7-7	5.26	5.53	4.2	4.3	1.4	1.4	80.4
1.5	9-19	4.83	4.4	4.5	4.2	1.31	1.3	83.8
2.5	5-31	10.77	9.86	5.3	4.9	1.75	1.3	106.9
2.5	8-4	10.21	10.62	4.7	4.8	1.85	1.9	144.1
2.5	8-27	13.76	13.68	4.8	4.5	1.78	1.8	105
3.5	7-30	18.55	17.67	5.3	5.2	2.74	2.6	141.5
3.5	9-13	11.12	11.98	4.5	4.3	2.01	2.1	94.6
3.5	9-24	21.5	23.71	5.3	5.4	2.93	3	112.9
4.5	7-7	5.83	5.89	3.6	3.5	1.66	1.7	108.1
4.5	8-17	19.83	19.44	5.5	5.6	2.8	2.8	120.4
4.5	11-8	14.61	14.08	5.4	ND ^d	2.39	2.5	181.5
5.5	7-25	26.45	26.66	5.8	6.3	2.96	2.9	125.9
5.5	7-25	22.61	21.1	5.7	5.6	2.93	2.9	169.3
5.5	8-12	31.47	30.76	6.2	6.5	3.03	3	157.2
7.5	5-18	36.53	ND	6.3	ND	3.34	ND	151.1
7.5	8-18	27.77	ND	5.8	ND	3.03	ND	146.6
7.5	10-19	18.45	ND	6	ND	2.71	ND	133.3
11.5	9-20	31.15	31.74	6.1	6.1	3.18	3.2	167.2
12.5	6-26	45.41	46.6	6.8	7	3.54	3.5	212.6
14.5	7-31	52.28	53.08	7.6	7.6	3.63	3.5	167.3

^aDate when killed (M = Month, D = Day).

^bTesticles for each bear labeled A and B because side was unknown.

^cSTD = Seminiferous tubule diameter.

^dND = No data.

Testicle mass was related linearly to age ($r^2 = 0.80$, $P = 0.05$; Fig. 16), whereas the relationship between age and seminiferous tubule diameter was non-linear.

Seminiferous tubule diameter increased rapidly in bears between 1.5 and 5.5 years of age, then increased less rapidly in bears older than 6.5 years (Fig. 17). Seminiferous tubule diameter appeared to asymptote at about 10-12 years of age (Fig. 17).

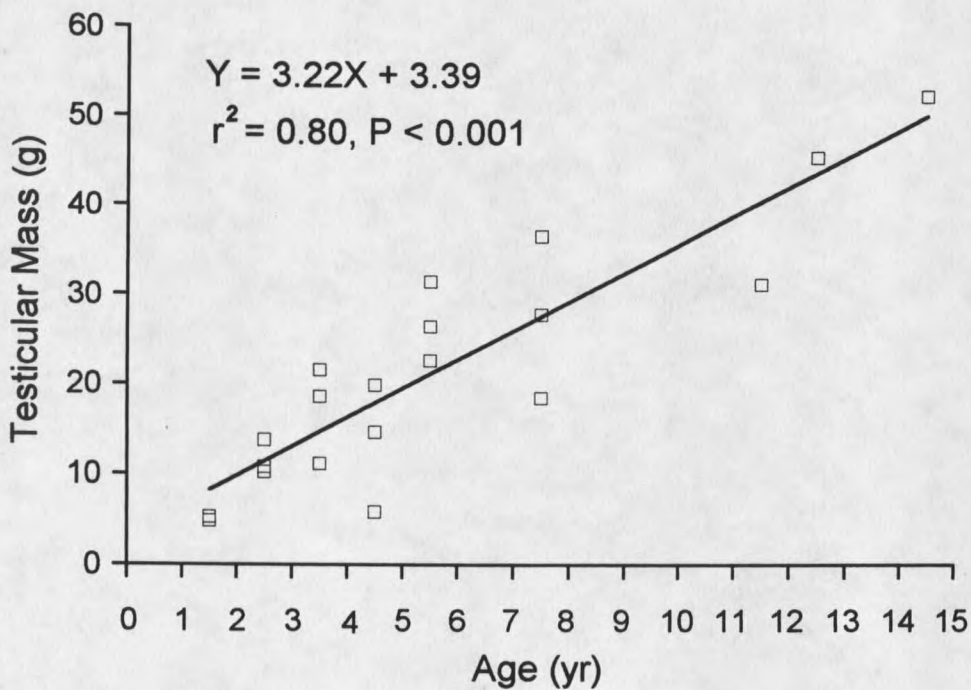


Figure 16. Age variation in testicle mass for male grizzly bears from Montana and Wyoming, 1978-1992.

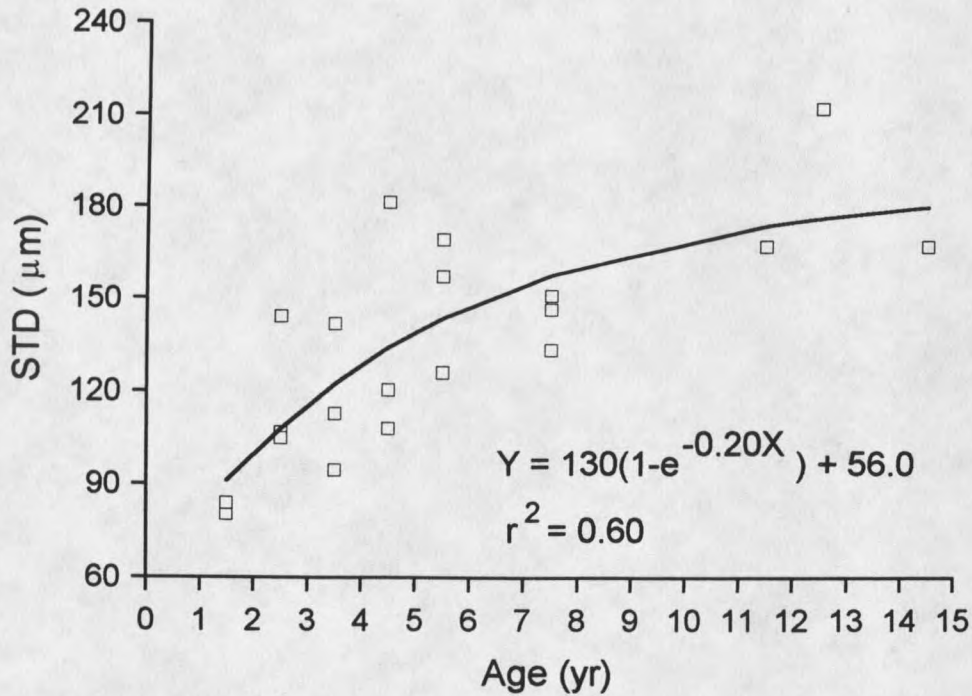


Figure 17. Growth curve of seminiferous tubule diameters (STD) in male grizzly bears from Montana and Wyoming, 1978-1992.

The youngest bear in which fully-formed spermatozoa were found in the lumen of seminiferous tubules was 3.5 years-old and killed in July. However, 2 other 3.5 year-olds (both killed in September) and three 4.5 year-old bears (killed in July, August, and November) did not have spermatozoa in their tubules. Therefore, I considered the grizzly bears in our study that were ≤ 4.5 years-old to be reproductively immature. Only 1 of the 11 bears that were ≤ 4.5 years-old had spermatozoa in the seminiferous tubules, whereas 8 of the 9 bears ≥ 5.5 years-old did. The single bear > 4.5 years of age without spermatozoa was a 7.5 year-old bear killed in October. The proportion of bears < 5.5 years-old with and without spermatozoa

was significantly different than the proportion in bears ≥ 5.5 -years-old ($X^2 = 13.5$, $df = 1$).

Testicular mass, testicular volume, and seminiferous tubule diameter were smaller ($P = 0.05$) in immature bears than in mature bears (Table 7). Mature males had testicles that weighed more than 25 g each (mean = 32.63 g) and seminiferous tubule diameters of at least 150 μm (mean = 158.87 μm). Mean testicle mass and seminiferous tubule diameter of immature male grizzly bears were 12.39 g and 116.29 μm , respectively.

Table 7. Mean (\pm SE) testicle mass, volume, and seminiferous tubule diameter (STD) for immature and mature grizzly bears in Montana and Wyoming, 1978-1992.

Age class ^a	<i>n</i>	Testicle mass (g)	Testicle volume (cm^3)	STD (μm)
Immature (≤ 4.5 years old)	11	12.4 \pm 1.8 ^a _b	96 \pm 18.2 ^a	116 \pm 8.9 ^a
Mature (≥ 5.5 years old)	9	32.6 \pm 3.2 ^b	267 \pm 26.1 ^b	158 \pm 7.5 ^b

^aBased on the presence (mature) or absence (immature) of spermatozoa in the lumen of the seminiferous tubules.

^bDifferent letters within a column indicate a significant difference ($P < 0.05$).

Data for mature bears were grouped into 2 seasons: May through mid-July (the breeding season) and mid-July through November (the post-breeding season). Testicle mass and volume and seminiferous tubule diameter did not differ ($P < 0.05$) between the seasons (Table 8), although my sample sizes were small.

Table 8. Mean (\pm SE) testicular mass and volume, and seminiferous tubule diameter (STD) in mature grizzly bears killed during May through mid-July and mid-July through November in Montana and Wyoming, 1978-1992.

Date	<i>n</i>	Testicle mass (g)	Testicle volume (cm ³)	STD (um)
May through mid-July	2	20.8 \pm 4.11 ^a	250 \pm 30.0 ^a	131.82 \pm 11.30 ^a
Mid-July through November	7	22.41 \pm 2.51 ^a	327 \pm 30.6 ^a	138.05 \pm 6.30 ^a

^aSame letters within a column indicate no significant difference ($P > 0.05$).

Discussion

Effects of season on gonadal activity in black bears (Erickson et al. 1964, McMillin et al. 1976, Reynolds and Beecham 1980, Horan et al. 1993, Garshelis and Hellgren 1994), and brown and grizzly bears (Erickson et al. 1968, Pearson 1975, Tsubota and Kanagawa 1989) are well documented. Few studies, however, have investigated testicular and seminiferous tubule growth with age. My analysis of data in Tsubota and Kanagawa (1991) indicated that testicle mass in Hokkaido brown bears is not related linearly with age ($n = 24$, $r^2 = 0.47$); rather testicular mass appeared to reach an asymptote in 8-10 years. In contrast, I found a linear increase in testicle mass for bears ≤ 14.5 years-old (Fig. 19). Two bears, ages 15 and 18, greatly reduced the slope of the line in Tsubota and Kanagawa's data. The lack of bears older than 14.5 years could explain why testicular mass did not reach an asymptote in our study.

Parenthetically, my results indicate that studies designed to investigate age or seasonal

variation in grizzly bear reproductive biology could biopsy testicular parenchyma without regard to testicular location.

My findings do not support the general trend of testicular growth in spring and regression in autumn. However, only 3 of our bears were killed in May and June, and only 6 were killed in September through November (Table 6). Low sample sizes and temporally limited data made it difficult to interpret seasonal trends.

In my study, mean testicular mass, volume, and seminiferous tubule diameters of immature and mature grizzly bears differed (Table 7), which is consistent with data reported by Tsubota and Kanagawa (1991) for Hokkaido brown bears. Mean testicular mass and seminiferous tubule diameters in the immature grizzly bears of our study were consistently larger than those of immature Hokkaido brown bears. However, in my study, mean testicular mass and seminiferous tubule diameters in mature grizzly bears were similar to those in mature Hokkaido brown bears. The reason for the discrepancy in the immature bears is not readily apparent except that Tsubota and Kanagawa (1991) used a different method than I did for measuring testicular size.

Tsubota and Kanagawa (1991) studied age of sexual maturity in male Hokkaido brown bears and concluded that sexual maturity, based on the presence of fully-formed spermatozoa in the lumen of seminiferous tubules, occurred between 2 and 5 years of age. Erickson et al. (1968) and Pearson (1975) reported that fully-formed spermatozoa first appeared in seminiferous tubules of brown bears in Alaska and

grizzly bears in the Yukon at approximately 4.5 and between 5 and 7 years of age, respectively. These data generally agree with my results, except for the captive 2 year-old Hokkaido brown bears showing active spermatogenesis (Tsubota and Kanagawa 1991). The youngest bear in my study that showed spermatogenesis was 3.5 years old. Jonkel and Cowan (1971), Rogers (1976), and Elowe and Dodge (1989) have implicated nutrition as an important influence on reproduction in the American black bear. They found that reproductive rates of female black bears declined when mast or berry crops were poor the previous fall. Age of sexual maturity, breeding interval, and litter size were all altered by nutritional factors. An increased nutritional plane may explain why male Hokkaido brown bears reach sexual maturity earlier than male grizzly bears in the continental United States. An examination of short-term gonadal responsiveness to nutritional factors in brown bears warrants further study due to the profound impact on population dynamics.

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