

University of Nevada, Reno

Relationships between Army Cutworm Moths and Grizzly Bear Conservation

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in
Ecology, Evolution, and Conservation Biology

by

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December, 2009

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THE GRADUATE SCHOOL

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Relationships Between Army Cutworm Moths And Grizzly Bear Conservation

be accepted in partial fulfillment of the
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ABSTRACT

Army cutworm moths (*Euxoa auxiliaris*) are native to North America and are both agricultural pests and an important food for grizzly bears (*Ursus arctos horribilis*). The moths migrate from low elevations in the Great Plains and Intermountain West to high elevations in the Rocky Mountains where they aggregate in talus and are consumed by bears by the millions during summer.

There are conservation implications of moths as food for bears. Previous studies determined the moths are the richest bear food in the Greater Yellowstone Ecosystem (GYE). Bears that gorge on moths can consume half of their yearly energy in about 30 days. Moths occur in remote areas rarely visited by humans and are available through autumn. When high elevation foods like moths and whitebark pine (*Pinus albicaulis*) seeds are abundant, bears forage for them in these remote areas. The availability of food in autumn influences bear litter size. When these foods fail, bears forage widely and get into more fatal conflicts with humans. Human-caused bear mortality is the major threat to bears. Balancing recruitment and mortality is essential to bear conservation.

Research on the moths is critical to understanding their availability to bears and their roles in ecosystems. I reviewed literature about the moth's ecology and its interaction with bears. I then describe research that may advance our understanding of this interaction. The moth's migration is unusual. It migrates across latitudes whereas most other pestiferous moths in North America migrate latitudinally. Migration across latitudes appears to be easier than migration across longitudes, but how these moths

determine longitude is unknown. The moth's migration and reproductive activity were thought to be incompatible, but I found that this is not the case.

I investigated population structure in the moth using microsatellites so I might describe more clearly their migration and the scale at which it may influence their availability to bears. The results indicate the moths are panmictic. This is favorable for the long-term persistence of the interaction between moths and bears. Population structure, indicative of site fidelity, would make the moths susceptible to local perturbations at low elevations and likely result in corresponding extirpations at high elevation sites. The Rocky Mountains appear not to be a barrier, and the moths may migrate from the west to the mountains as well as from the east.

I studied whether moths, whose larvae may be sprayed with organochlorine, organophosphate and pyrethroid pesticides, contain chemical residues which could be toxic to bears or bioaccumulate in bears. The results of these analyses show that moths contain very low levels of contaminants, but these levels are unlikely to be toxic to or bioaccumulate in bears.

I modeled moth and bear habitat using geospatial variables extracted from locations where bears forage for moths. Elevation, geology, and Landsat TM imagery describe areas currently used by moths and bears in the GYE and predict areas which may be suitable for moths and into which bears may expand within the GYE. Slope, aspect, and heat-load also were significant predictors of these sites but did not contribute as much to model fit to the data. The model may reflect bear preferences for foraging for moths more than the distribution of moths in high elevations because the data used to generate the model are based on locations where bears feed on moths, not on moth locations alone.

ACKNOWLEDGEMENTS

This dissertation would not have been possible without the assistance of many people and organizations. My advisor Peter Brussard and my committee members Scott Mensing, Charles Schwartz, Peter Weisberg and David Zeh have each offered their time, knowledge, and guidance. Veronica Kirchoff shared her expertise in the genetics laboratory and was pivotal in my success. Mary Peacock provided insights and work space in her lab. This project was large in scale and logistically complicated; the field work required would not have been possible without the incredible support of Scott Hampton, who helped me for three field seasons, as well as the help of Natalie Dawson, Tyler Free, Carol Gibbs, Jason Hicks, Rebecca Key, Chris McQueary, Corey Van Stratt. S. Hampton also provided critical support in the lab and Alyson Andreason, David Badley, Michele Coker, Ann DiSalvo, Julie Ellsworth, J. Hicks and Steve Van Slyke provided additional help in the lab. Kerry Gunther of the Yellowstone National Park Bear Management Office was a consistent source of support. Mark Haroldson of USGS Interagency Grizzly Bear Study Team provided logistical support throughout the project. Cecily Costello graciously provided moth samples from New Mexico. Kim Barber of the Shoshone National Forest shared insights and helped with logistics. The USGS Columbia Environmental Research Center analyzed moth samples for pesticide residues. Montana State University Agricultural Extension Agents played a critical role in helping me obtain moths throughout Montana. My family, especially my parents Bruce and Betty Robison, has provided me with amazing support throughout my life and this project. My sister Heidi Robison helped me in the field and has edited many works

related to this project. My husband Steve Van Slyke has been patient and supportive throughout my dissertation research. Fellow graduate students Lisa (Cali) Crampton, Claudia Funari, Chris Kratt, Helen Neville, and Lily Peacock were a consistent source of collegial support and outdoor companionship. This project was expensive and would not have been possible without the generous support of the Rob & Bessie Welder Wildlife Foundation, Yellowstone Park Foundation, International Bear Association, American Museum of Natural History, Sigma Xi, the Wyoming Chapter of the Wildlife Society, Greater Yellowstone Coordinating Committee, the University of Nevada, Reno Graduate Student Association Research and Travel Grants. Finally, this dissertation is in memory of Kirk Inberg and Chris Mills who each studied the relationship between moths and bears and passed away before their time.

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CHAPTER 1

Army cutworm moth ecology spans ecosystems and influences grizzly bear conservation

INTRODUCTION

Army cutworm moths (*Euxoa auxiliaris*) are migratory noctuid moths that are native to North America, and their ecology is regional in scale. They range from Kansas to California and from central Canada to New Mexico (Figure 1). During their one-year lifespan they play important ecological roles in both the low elevations of the Great Plains and Intermountain West where they are agricultural pests and in the high alpine zone of the Rocky Mountains where they pollinate flowers and are preyed upon by grizzly bears (*Ursus arctos horribilis*) and other species (Pruess 1967, Mattson *et al.* 1991, French *et al.* 1994, Kevan and Kendall 1997, White *et al.* 1998a,b). While the moths are at high elevations they are particularly important to grizzly bears; the bears can consume enough moths in 30 days to meet half of their yearly energy needs (White 1996, White *et al.* 1999).

Studies of *E. auxiliaris* in its low and high elevation habitats have been conducted largely independently by entomologists and wildlife ecologists; interdisciplinary studies are rare in the literature. My goals in this chapter are to synthesize these bodies of literature, make them available to a wider audience of ecologists, and highlight research

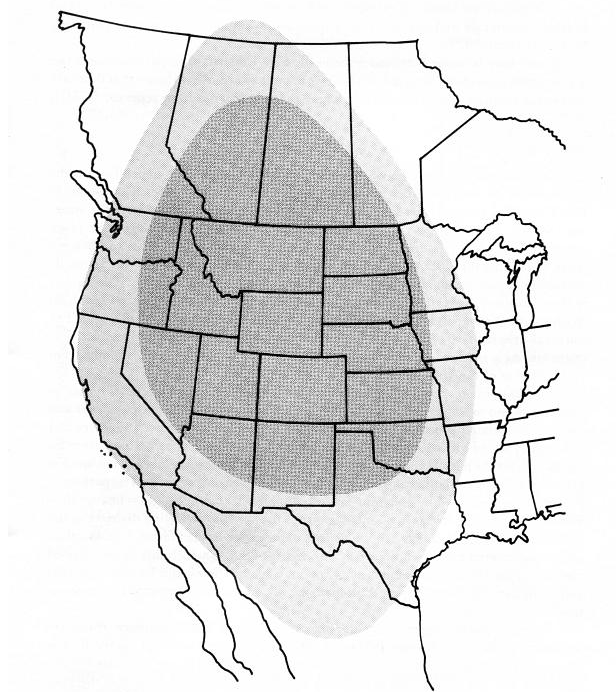


Figure 1. Army cutworm moth distribution in North America. The light gray area represents the probable maximal range of moths, and the dark gray area represents areas where outbreaks of moth larvae might occur (from Burton *et al.* 1980).

that aids our understanding of moth ecology and the availability of moths to grizzly bears. Herein I review findings discussed in the peer-reviewed and gray literature about *E. auxiliaris* ecology, life history, systematics and its interaction with bears and I point to directions that may advance our understanding of the relationships between moths and grizzly bear conservation.

TAXONOMY, SYSTEMATICS, AND BIOGEOGRAPHY

The genus *Euxoa* belongs to the Noctuoidea, the largest superfamily within the order Lepidoptera, and to the Noctuidae, the largest family within the order, which contains

~25,000 described species (Wagner 2001, Mitchell *et al.* 2006). The earliest lineages of Noctuoidea arose in the Tertiary period and were probably tree dwellers (Mitchell *et al.* 2006). The radiation of the group of Noctuidae to which *Euxoa* belongs is postulated to have tracked the expansion of open areas and herbaceous floras during that period (Mitchell 2006). The ancestor of *Euxoa* was probably adapted to open arid lands and, in North America, likely originated in the mid-Tertiary (Lafontaine 1981). Forest-dwelling then became a derived condition in the genus (Lafontaine 1982). During the Pleistocene epoch, successive glacials and interglacials caused contractions and expansions of arid lands and corresponding expansions and contractions of woodlands (Lafontaine 1982). Although species of *Euxoa* in North America are categorized into arid land, forested, or widespread types (Lafontaine 1982), the larvae of many *Euxoa* species currently inhabiting North America require relatively dry soil conditions, and their ranges are confined to the dry western part of the continent (Lafontaine 1982, Hardwick and Lefkovitch 1971).

The resolution of species within the genus *Euxoa* has challenged taxonomists since the group was studied in the early 1900s (Wooley-Dod 1905, Burton *et al.* 1980). Hardwick (1970) predicted that this genus in North America eventually will include ~200 species. Hardwick (1970) described *Euxoa* as particularly challenging to classify, “Probably no other genus in the Noctuidae exhibits such a high degree of intraspecific variability which is often coupled with an amazing lack of structural characters by which species may be distinguished.” The most common species of *Euxoa* usually vary most in maculation and coloring, and similar patterns are repeated among different species within the genus (Hardwick 1970). There also is evidence of interspecific hybridization in some species groups within the genus (Hardwick 1970). Hardwick (1970) suggests that both of these

facts may be explained best by the fact the genus is in “a state of great evolutionary mutability.” The recent finding of microsatellite families, groups of non-coding genes with similar or identical repetitive flanking regions, in *E. auxiliaris* (H. Robison 2009, Chapter 2) may indicate, as Zhang (2004) suggests for other Lepidoptera, that microsatellites are in an early stage of evolution in this group.

Approaches to resolve the relationships within *Euxoa* include studies of egg microstructure (Hudson 1973, Salkeld 1976), electrophoretic studies of egg proteins (Hudson 1973), serological relationships between egg antigens (Hudson 1973), and morphological studies (Lafontaine 1987 and references therein). Currently, 180 species have been described within the genus in North America (Lafontaine 1981, Lafontaine 1987 and references therein).

E. auxiliaris is a member of the subfamily Noctuidae (Lafontaine and Fibiger 2006), most species of which associate with particular habitat types more than specific plants (Mitchell *et al.* 2006). Many species within Noctuidae are polyphagous and strongly dispersive (Mitchell *et al.* 2006). *E. auxiliaris* is categorized as a widespread species, and it inhabits both open arid lands and forested areas (Lafontaine 1982).

Latin binomials assigned to *E. auxiliaris* have been revised a number of times over the years (Table 1, Burton *et al.* 1980). From the late 1800s through the early 1900s, the army cutworm moth was regarded as a mixture of several species within the genus *Chorizagrotis* (Cook 1930a). During this time, five color forms were described for what is now known as the army cutworm moth, *E. auxiliaris*: *E. auxiliaris*, *E. introferens*, *E. agrestis*, *E. montanus*, and a melanic form (Mansbridge 1897, Pruess 1967, Cook 1930a) (Figure 2). Some of these forms were originally considered distinct species (Smith 1890, Pruess

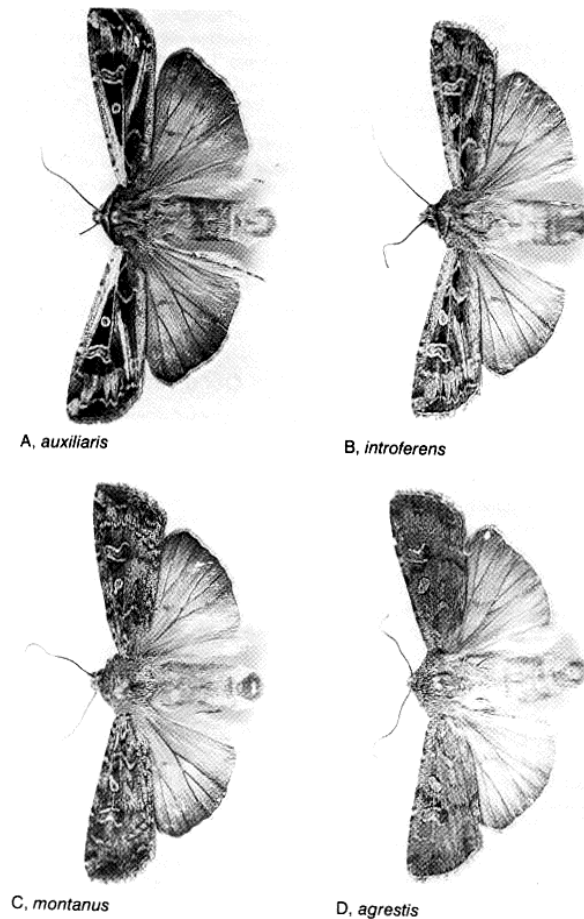


Figure 2. Color morphs of the *E. auxiliaris* once described as different species. A. *Euxoa* “*auxiliaris*”, B. *Euxoa* “*introferens*”, C. *Euxoa* “*montanus*”, D. *Euxoa* “*agrestis*.” The melanic form is not shown (from Burton *et al.* 1980).

1967), but their validity as species was reconsidered later (Strickland 1916, Cook 1930a, Pruess 1967). Cook (1930a) stated that color morphs are likely plastic characters because they varied with rearing temperature. Pruess (1967) found the only morphological characters that differed significantly between these forms were size and weight. Recently, analysis of microsatellite loci among color morphs within the species (H. Robison, Chapter 2) supports the case that there are no species level differences among these color forms.

Table 1. Latin binomials given to the army cutworm moth.

<i>Agrotis auxiliaris</i>	Grote (1873)
<i>Agrotis introferens</i>	Grote (1875)
<i>Agrotis auxiliaris</i> var. <i>agrestis</i>	Grote (1877)
<i>Chorizagrotis auxiliaris</i>	Smith (1890)
<i>Chorizagrotis introferens</i>	Smith (1890)
<i>Agrotis introferens</i>	Hampson (1903)
<i>Agrotis agrestis</i>	Hampson (1903)
<i>Euxoa introferens</i>	Smith (1904)
<i>Chorizagrotis inconcinna</i>	Wolley-Dodd (1905)
<i>Chorizagrotis terrealis</i>	Wolley-Dodd (1905)
<i>Euxoa auxiliaris</i> ab. <i>tegaris</i>	Strand (1915)
<i>Chorizagrotis auxiliaris introferens</i>	Barnes and McDunnough (1917)
<i>Chorizagrotis auxiliaris</i> form <i>tegaris</i>	Draudt (1924)
<i>Chorizagrotis auxiliaris</i> form <i>montanus</i>	Cook (1930a)
<i>Chorizagrotis auxiliaris</i> form <i>agrestis</i>	McDunnough (1938)
<i>Euxoa auxiliaris</i>	Hardwick (1970)

LOW ELEVATION ECOLOGY

E. auxiliaris is univoltine (*i.e.*, it has one brood per year) (Figure 3). Adult females oviposit ~2,000 eggs (in groups of one to three) onto the surface or just below the surface of tilled or loose soil during late September and early October (Cooley 1916, Strickland 1916, Pruess 1967, Burton *et al.* 1980). Mature eggs of *Euxoa* species measure 0.46 mm in length by 0.66 mm in width (Salkeld 1976). Shortly after oviposition, both sexes die.

Since *E. auxiliaris* eggs and plant seeds both require similar moisture and temperature to hatch and germinate, larvae are able to feed on emerging plants in the fall and spring (Burton *et al.* 1980). Larvae usually feed on plants at the soil surface and above the plant's apical meristem, so they usually do not kill plants but do stunt their growth. Larvae feed on a wide variety of plants (Strickland 1916) (Table 2) until early winter

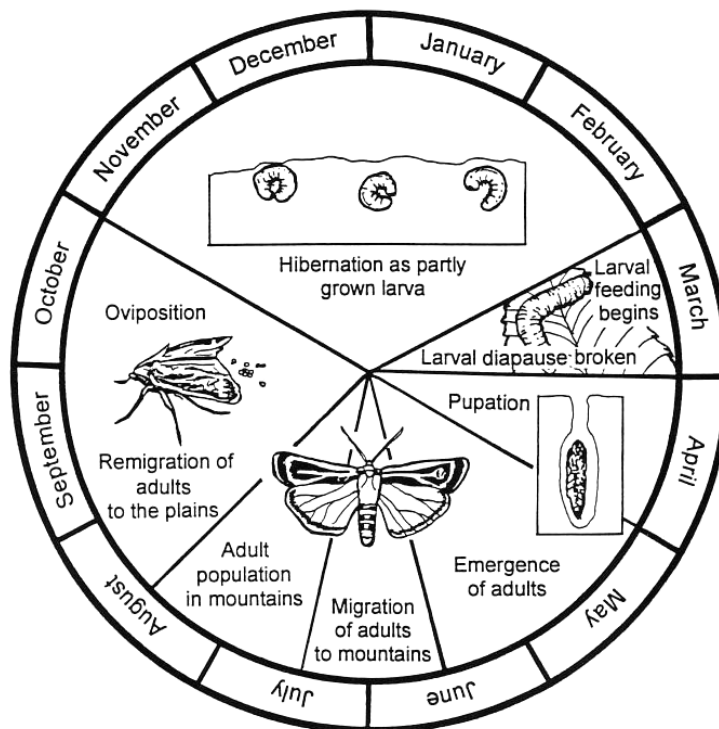


Figure 3. Army cutworm moth life history (from White 1996).

(Burton *et al.* 1980). Wilcox (1898) found that larvae also will eat plant stubble and exposed roots, often the only plant tissue found in tilled or disked fields. When food is scarce, larvae will feed on plants below the soil surface, killing them, and, in extreme circumstances, will eat each other (Burton *et al.* 1980).

Larvae feed in the early evening and into the night. They feed on plants in an area until the forage is depleted and then march together up to 5 km (Wilcox 1898) to find new food; this mass movement is the behavior that led them to be called the “army” cutworm. Larvae usually march to the northwest to find a new field, but their behavior apparently varies with the position of the sun and the time of the day (Burton *et al.* 1980). During outbreaks, the density of larvae can reach up to 1500 larvae/m² (Strickland 1916).

Table 2. Plants consumed by *E. auxiliaris* (compiled from Wilcox 1898, Strickland 1916, and Burton *et al.* 1980)

Scientific name	Common name
<i>Acer</i> spp.	maple seedlings
<i>Agrostis</i> spp.	bentgrass
<i>Allium</i> spp.	garlic, onion, chive, and allies
<i>Apium graveolens</i>	wild celery
<i>Armoracia</i> spp.	horseradish
<i>Astragalus</i> spp.	milkvetch
<i>Avena</i> spp.	oat
<i>Balsamorhiza sagittata</i>	arrowleaf balsamroot
<i>Beta vulgaris</i>	beet
<i>Bouteloua</i> spp.	grama
<i>Brassica oleracea</i>	cabbage, broccoli, brussel sprouts
<i>Bromus carinatus</i>	California brome
<i>Buchloe dactyloides</i>	buffalograss
<i>Calamagrostis canadensis</i>	bluejoint
<i>Capsella bursa-pastoris</i>	shepherd's purse
<i>Chenopodium album</i>	lambsquarters
<i>Cirsium</i> spp.	thistle
<i>Cleomella</i> spp.	stinkweed
<i>Dalea purpurea</i>	purple prairie clover
<i>Delphinium bicolor</i>	little larkspur
<i>Descurainia sophia</i>	flixweed, herb sophia, tansy mustard
<i>Echinops</i> spp.	globethistle
<i>Elaeagnus angustifolia</i>	Russian olive
<i>Elymus</i> spp.	wheatgrass
<i>Erysimum repandum</i>	spreading wallflower
<i>Fragaria</i> spp.	strawberry
<i>Helianthus nutallii</i>	Nuttall's sunflower
<i>Hordeum leporinum</i>	hare barley
<i>Hordeum pusillum</i>	little barley
<i>Leymus</i> spp.	wildrye
<i>Linum lewisii</i>	Lewis flax
<i>Lupinus argenteus</i>	slivery lupine
<i>Lycopersicon esculentum</i>	garden tomato
<i>Medicago sativa</i>	alfalfa
<i>Melilotus</i> spp.	sweetclover
<i>Onobrychis viciaefolia</i>	sainfoin
<i>Opuntia polyacantha</i>	plains pricklypear
<i>Phleum pratense</i>	timothy
<i>Pisum sativum</i>	garden pea
<i>Poa</i> spp.	bluegrass
<i>Prunus serotina</i>	black cherry
<i>Prunus</i> spp.	plum

<i>Raphanus</i> spp.	radish
<i>Rheum</i> spp.	rhubarb
<i>Ribes</i> spp.	currant
<i>Rubus</i> spp.	blackberry
<i>Salix tristis</i>	prairie willow
<i>Sisymbrium</i> spp.	hedgemustard
<i>Solanum tuberosum</i>	Irish potato
<i>Taraxacum officinale</i>	common dandelion
<i>Trifloium</i> spp.	clover
<i>Triticum</i> spp.	wheat
<i>various species</i>	dry weed roots
<i>Vicia</i> spp.	vetch
<i>Zea mays</i>	corn

During the day larvae hide under dirt clods or soil, so heavily infested fields may look uninfested during the day. Immature larvae over-winter in underground cells and develop through seven instars. Heavy spring rains cause larvae to drown in their underground cells, and the abundance of larvae is lower after wet springs (Blodgett 1997). In the spring, the larvae surface, begin feeding on emerging plants (Table 2), and then complete their larval development. Once mature, the larvae burrow into underground cells a few inches below the soil surface where they pupate (Burton *et al.* 1980).

Larvae have been controlled using the following methods: digging water filled trenches in front of migrating larvae (late 1890s); baiting larvae with arsenic-tainted bran mash (1915-1930s); leaving soil unworked (*i.e.*, leaving the ground with a thick crust) during the moths' oviposition period (1940s); and using chlorinated hydrocarbon insecticides such as endrin and toxaphene (1950s). Currently, a variety of organophosphate, carbamate, pyrethroid, biological (*e.g.*, *Bacillus thuringiensis*), and, less commonly, organochlorine pesticides are used to control outbreaks of larvae

(Robison *et al.* 2006). Parasites (*e.g.*, ichneumonid and braconid wasps and tachinid flies), predators (*e.g.*, blackbirds [*Euphagus cyanocephalus*, *Agelaius phoeniceus*], bluebirds [*Sialia currucoides*], robins [*Turdus migratorius*], meadowlarks [*Sturnella neglecta*], chickens [*Gallus gallus domesticus*], and ground beetles [Carabidae]), disease, and weather naturally decrease populations of larvae.

From 1999-2003, methods were developed to forecast *E. auxiliaris* larvae abundance in the Great Plains and Intermountain West of the USA and Canada in the spring. These methods were based on the numbers of moths trapped in pheromone traps in the late summer and fall, degree day accumulation from January 1 (for occurrence of the larval stage), and precipitation data from May through June (Blodgett *et al.* 2003). The regional cutworm monitoring program was designed to enable farmers to focus their monitoring in years and areas when their crops are at risk from damaging populations of larvae and to reduce unwarranted pesticide applications.

MIGRATION

In the early 1900s, scientists thought that *E. auxiliaris* had two broods per year (Gillette 1904) because the moths were abundant in low elevations in the late spring, absent in the summer, and then present again, although in fewer numbers, in the fall. Strickland (1916) suggested the moths aestivate during the hottest part of the summer, which may give the appearance that they are double-brooded when they are not. Pepper (1932) suggested that the moths might migrate to mountains in the summers based on observations of unidirectional flight by the moths, the inability of caged moths to survive warm summers in low elevations, and the moths' ability to survive the summer when

held at low temperatures (3° C). Pruess (1967) also held moths in cages at ambient temperatures in the Great Plains and found that few to none survived. Jacobson and Blakeley (1959) and Pruess (1963) observed similar influences of temperature on moth longevity. Additionally, from around the turn of the century through the 1950s, scientists collected the moths in high elevations in the Rocky Mountains during the summer (Gillette 1989, Gillette 1904, Walkden 1950, Chapman *et al.* 1955).

Scientists wondered if the moths were capable of a migration of that scale. In the 1960s Pruess and colleagues (Koerwitz and Pruess 1964) performed laboratory studies with moths flying in a flight mill. They found that the moths were capable of flying up to 300 km in 65 hours, and the longest uninterrupted flight they recorded was 214 km. Later, Pruess (1967) conducted field studies in which he trapped and aged moths from the Great Plains to the Rocky Mountains and determined that the moths migrate to high elevations in the Rocky Mountains and remain there throughout the summer. This finding confirmed what had been suspected about their ecology (Hardwick 1970).

A number of other noctuids are also migratory, including species in the genera *Agrotis*, *Euxoa*, *Helicoverpa*, *Heliothis*, *Noctua*, *Ochropleura*, and *Spodoptera* (Oku 1983, Showers 1997). Although Hardwick and Lefkovitch (1971) described regular seasonal movements to be rare among species within the genus *Euxoa*, Oku (1983) describes the migratory habitat as “evolved particularly in the genus *Euxoa*” and cites several migratory species within the genus.

Most migrating insects migrate by flying either under their own power, by using favorable winds, or a combination of both. Insects powering their own flight are flying within their flight boundary layer (FBL). An insect’s FBL is the layer of air near the

ground, less than a few tens of meters wide, within which it can travel under its own power and control its direction of flight (Taylor 1974). Conditions in the atmosphere also influence insect migration. The planetary boundary layer (PBL) is the lowest 1-2 km of the atmosphere and is strongly influenced by the Earth's surface (Johnson 1995). The PBL can be convective during the day and stable at night. At night strong, steady winds called low-level jets (LLJs) develop, and when these winds are favorable, insects flying at night can leave their FBL and ride them (Gatehouse and Zhang 1995).

Agrotis ipsilon, a noctuid moth in the sister genus to *Euxoa*, migrates across latitudes in North America. Studies show it uses two strategies to migrate; it uses LLJs (200-1000 m in height) during its spring poleward migrations and uses lower-level winds (100-300 m in height) during its fall equatorward migration (Showers *et al.* 1993). Movements by *E. auxiliaris* are across longitudes as opposed to across latitudes, and although there is some evidence that the moth may use winds during its migration (K. Pruess unpub. data, K. Pruess pers. comm.), the influence of weather patterns on the moth's movements is not well understood.

IMPETUS TO MIGRATE

Pruess (1967) reasoned that moths migrate from the Great Plains to the Rocky Mountains to escape the high temperatures on the Plains and to seek refuge and nectar resources in the cooler climate of the Rocky Mountain alpine zone. Oku (1983) who has studied a different species of *Euxoa* with similar migratory behavior and who has reviewed aestivation and migration in noctuid moths, suggests that "summer diapause" in the adult stage often is associated with long distance migration, common in univoltine species in

temperate areas, associated with seasonal migration, and always directed to alpine zones. Oku (1983) suggests that noctuid moths undergoing summer diapause as adults migrate to high elevations to escape high temperatures in low elevations, but more specifically, they do so when their low elevation habitats are arid. Although *E. auxiliaris* fits with the high temperature and arid components of this hypothesis, they do not fit with the accompanying stipulation of reproductive diapause because the moths are still reproductively active.

Although biologists who have studied *E. auxiliaris* to date agree that temperature (Pruess 1967, Hardwick and Lefkovitch 1971, Oku 1983) and aridity (Hardwick and Lefkovitch 1971, Oku 1983) may motivate the migration of the moth, the physiological and ecological mechanisms the moths use to trigger migration remain unknown. Additionally, *E. auxiliaris* migration appears to vary temporally with latitude (Pruess 1967). Moth migration appears to be more pronounced at lower than at higher latitudes. In latitudes between 30-40° N moth migration to the mountains is earlier in the spring and their return to the plains is later in the fall than at latitudes between 40-50° N (Oku 1983). North of 50° N there is no clear migration pattern (Oku 1983).

Migratory animals use one or more compasses to orient their flight. A sun compass is based on time-compensation derived from patterns of light polarization; a star compass provides geographic information to migrants at night as the stars rotate; a magnetic compass involves use of magnetic gradients of the Earth and usually influences migrations to the poles and the equator, and a genetic compass may be involved in species that do not have the opportunity to learn migration routes from their parents (Akesson and Hedenstrom 2007). Discerning latitude involves sun, celestial, and geomagnetic compasses and appears to be easier for migrants to discern than longitude (Akesson and Hedenstrom 2007, Gould

2008). The migratory ecology of other North American noctuid species (e.g. *A. ipsilon* [Showers *et al.* 1993], *Helicoverpa zea*, *Spodoptera frugiperda* [Westbrook 2008], *Pseudaletia unipuncta* [McNeil *et al.* 1995]) is better known than that of *E. auxiliaris*. Most of these species migrate latitudinally, whereas *E. auxiliaris* migrates longitudinally, but how *E. auxiliaris* determines longitude and migrates across longitudes is unknown.

MIGRATION TO AND FROM THE MOUNTAINS

E. auxiliaris flies westward to the Rocky Mountains from the Great Plains and Intermountain West in early late spring/early summer. A recent population genetics study indicates that the moths are panmictic or nearly so, and this suggests that the moths also may migrate eastward toward the Rocky Mountains from the west (H. Robison, Chapter 2). Koerwitz and Pruess (1964) found that newly-emerged moths contain 5-15% lipid and found that unfed moths could at most fly 18 km before stopping. Newly-emerged moths fed prior to flying commonly flew over 80 km and occasionally up to 214 km in a single flight. These findings show that the moths require nectar to fly long distances during their migration to the mountains. Various studies indicate that the moths feed on nectar and fly low to the ground in the evenings while en route to the mountains (Cook 1930b, Pepper 1932, Pruess 1967, Lavigne 1976, Kevan and Kendall 1997).

After spending the summer in the mountains, the moths begin migrating back to the Great Plains and Intermountain West from late August through the beginning of October. Kevan and Kendall (1997), who studied moths in high elevations in Colorado, found that *E. auxiliaris* accumulates fat while two *Euxoa* that are residents in alpine areas do not. They also suggest that the fat *E. auxiliaris* accumulates is for migration and for

“reproductive maturation.” Working in Montana, White *et al.* (1998b) also found that *E. auxiliaris* accumulated lipids and also suggested that this indicated the moths’ preparation for migration to low elevations. Based on their findings and those of Koerwitz and Pruess (1964), White *et al.* (1998b) suggested that moths may be using different strategies on their spring and fall migrations – feeding on plant nectar during their early summer migration and powering themselves off of lipids stored over the summer during their fall migration.

However, it appears that the lipids the moths store may not be sufficient to fuel their migration back to the plains. White *et al.* (1998b) found that the moths contained enough fat to power their flight back to low elevations up to a distance of 140 km, but admitted that this distance falls short of the Great Plains and that other factors, such as the moths using prevailing winds to facilitate their flight, might play a role in their migration. Additionally, Cook (1927) pointed out that various species of rabbitbrush (*Chrysothamnus* spp.) are in bloom during the timing of the fall flight and are likely important to the moths during that time, so it is possible that the moths are using both fat stores and rabbitbrush nectar during their return flight.

In fact, it may be opportune for moths to take advantage of nectar sources during their fall migration. Migrants save energy if, while traveling over benign environments, they avoid long flights with heavy fuel loads and instead divide their flights into shorter segments with lower fuel loads (Akesson and Hedenstrom 2007). Pruess (unpub. data, pers. comm.) suggests that perhaps the moths do not use their fat stores or consume nectar for energy while they migrate back to low elevations but may instead take advantage of westerly weather fronts to power their migration (Pruess and Pruess 1971, Pruess unpub. data) and use their fat stores for egg development.

Migrating moths may not have fidelity to specific high or low elevation areas. Byers *et al.* (1987) suggested that the moths may not always return to areas of their origin, based on the lack of consistency of trap catches versus their location. Pruess (1967), based on the absence of clines in the morphological characters of moths collected west to the Rocky Mountains, suggested that the moths he collected from the Great Plains to the Rocky Mountains could constitute a continuous gene pool.

Recently, analysis of variation at microsatellite loci developed for *E. auxiliaris* supports the idea that moths from various locations within their range and from either side of the Continental Divide do indeed interbreed (H. Robison, Chapter 2). This result supports the suggestions of Pruess (1967) and Byers *et al.* (1987) and the observation of Hardwick and Lefkovitch (1971) who suggested that the Rocky Mountains may not be a barrier to migration for various species of *Euxoa* based, in part, on the observations that similar associations of sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus* spp.), and ponderosa (*Pinus ponderosa*) or pinon (*Pinus monophylla*) pine are home to the same assemblages of species within the genus.

HIGH ELEVATION ECOLOGY

The moths reach high elevation talus slopes in the Rocky Mountains during late June and remain there through September. While in the alpine zone, moths forage on the nectar of alpine flowers during the evening and hide in the interstitial spaces of talus during the day. The moths aggregate in talus slopes at elevations between 2,768 – 3,680 m with slopes between 13-60 degrees that are found below large headwalls (White 1996, French

et al. 1994, O'Brien and Lindzey 1994). The rock comprising the talus at these sites typically measures 8 to 40 cm and lacks vegetation (Mattson *et al.* 1991).

While hiding in the talus the moths metabolize the nectar they consume and convert it into lipid (Pruess 1967, French *et al.* 1994, Kevan and Kendall 1997, White *et al.* 1998b). In June, moth lipid stores comprise ~13% of their body mass, and by late August and early September their lipid stores comprise up to 70-83% of their body mass (O'Brien and Lindzey 1994, Kevan and Kendall 1997, White *et al.* 1998b).

A moth eaten in late in the summer can provide 0.5 kcal for a predator, including grizzly and black bears (*Ursus americanus*), coyotes (*Canis latrans*), bats, mice, mustelids (species not identified) (French *et al.* 1994, White *et al.* 1998b, H. Robison, pers. observ.); ravens (*Corvus corax*), American pipits (*Anthus rubescens*), mountain bluebirds (*Sialia currucoides*), gray-crowned rosy finches (*Leucosticte tephrocotis*), black rosy finches (*Leucosticte atrata*), Clark's nutcrackers (*Nucifraga columbiana*) (French *et al.* 1994, White *et al.* 1998b); and wolf spiders (Lycosidae) (H. Robison, pers. observ.).

REPRODUCTION AND FLIGHT

Johnson (1969) described *E. auxiliaris* as a Class III migrant because it was thought to migrate to aestivation sites and enter an imaginal diapause upon reaching high elevations. Chapman *et al.* (1955), however, saw moths flying at dusk and suggested they might not aestivate in the mountains. Kevan and Kendall (1997) and White and colleagues (1998b) found the moths were active continuously and accumulated fat throughout the summer. Kevan and Kendall (1997) examined female moths ($n=512$) collected from July 26-August 23 and found only two had maturing eggs. From these data they concluded that "almost no

females of *Euxoa auxiliaris* showed ovarian development” in the alpine and that *E. auxiliaris* “delay[s] onset of reproductive maturation until the end of its summer residency in the alpine” (Kevan and Kendall 1997). Based on the above results, Kevan and Kendall (1997) describe the moth as a Class II migrant, which does not aestivate but has arrested development of its reproductive organs. Kevan and Kendall (1997) said the moths become “reproductively mature” only in late summer and this may start in the alpine. The idea that the moths do not become reproductively active until they migrate to low elevation has continued in the literature (White *et al.* 1998a).

The definitions of terms describing reproductive status are often not specified clearly in the literature on Noctuidae. Here I use “reproductively mature” to mean female moths are calling and mating. Recent studies of moths conducted later into the summer show that they become reproductively mature in high elevations as evidenced by sightings of hundreds of mating pairs in talus from August 23 through September 13, 2001 (H. Robison unpub. data). Moths also mate more than once while in the mountains, en route to, or in low elevations. Females collected from high elevations in late summer have contained up to two spermatophores, and females collected in low elevations in late summer have contained up to four spermatophores (H. Robison, unpub. data). Moth egg size ($n=131$) increases over the summer while moths are in high elevations, and egg development continues en route to and in low elevations (H. Robison, unpub. data).

Kevan and Kendall (1997) point out that the long pre-reproductive period of *E. auxiliaris* fits expectations of the “oogenesis syndrome” proposed by Johnson (1969) and that this syndrome is a common characteristic of other Class II migratory species. Oogenesis-flight syndrome is the idea that migration and reproductive development are

physiologically incompatible processes. Description of this syndrome stemmed from the observed pattern of pre-reproductive migration in many insect species (Sappington and Showers 1992, Gatehouse and Zhang 1995). However, some authors have challenged this idea (Baker 1978), and others have shed doubt on its general applicability (Sappington and Showers 1992). *Agrotis ipsilon*, a multi-voltine species in the sister genus to *Euxoa*, sometimes initiates migratory flight prior to reproduction and at other times while it is reproductively active, and this behavior varies across generations (Sappington and Showers 1992). *E. auxiliaris* migrates to the Rocky Mountains in the early summer prior to reproduction and thereby fits the oogenesis-flight syndrome as suggested by Kevan and Kendall (1997); however, during the moths' return migration to low elevations they migrate while they are reproductively active (*i.e.*, they continue to call and mate, and their eggs continue to develop en route) and do not fit the expectations of the syndrome.

ECOLOGY AND CONSERVATION SPANNING ECOSYSTEMS – ARMY CUTWORM MOTHS AND GRIZZLY BEAR CONSERVATION

Grizzly bears in the lower 48 states of the U.S.A. were listed as threatened under the U.S. Endangered Species Act in 1975 (USFWS 1993). The bears were listed because of concerns over their decline in population size due to excessive human-caused mortality (Craighead *et al.* 1995, Mattson and Reid 1991). Due to the success of conservation efforts, the bear population in the Greater Yellowstone Ecosystem (GYE) was delisted in 2007 (USFWS 2007b). A *Conservation Strategy* was, until September 2009, the guiding document for the bear's conservation since its delisting. The *Strategy* specified roles for managing the bears for the states in which the population resides – Montana, Wyoming,

and Idaho – as well as for the federal government (USFWS 2007a). The *Strategy* allowed bears to expand into biologically suitable and socially acceptable areas within and beyond the Primary Conservation Area (PCA) (Figure 4) prescribed for the bear. It also required monitoring the four major bear foods (moths, cutthroat trout [*Oncorhynchus clarki*], whitebark pine seeds, and winter-killed ungulates [*Bison bison*, *Cervus elaphus*, *Alces alces*, *Odocoileus hemionus*]) in the GYE (USFWS 2007) (Figure 5). Managing human-caused bear mortality was key to the *Strategy*. In response to a legal challenge a judge in Montana ruled on September 21, 2009 in favor of relisting the bear (USFWS 2009) and indicated the *Strategy* did not adequately address the security of bear foods in the face of climate change (New York Times 2009). Federal protections have been reinstated for the bear, and the *Strategy* is no longer in effect (USFWS 2009). Managing human-caused bear mortality and monitoring the four key foods, however, will remain important in any subsequent strategy to conserve the bear.

Key issues in species conservation and recovery include population resilience and population persistence through time. Weaver *et al.* (1996) describe grizzly bears as having less resilience than other Rocky Mountain carnivores (*e.g.*, wolves and cougars) because of their need for quality forage in the spring and fall, their low reproductive rate, and the strong philopatry of female offspring to maternal home-ranges. Grizzly bear population persistence is largely dependent on the survival and reproduction of adult female bears (Bunnell and Tait 1981, Eberhardt 1990, Craighead and Vyse 1996). Cub production is dependent on adequate pre-hibernation weight gain, and fat deposition by adult females (Rogers 1987) is positively correlated with increasing body mass of adult females and is

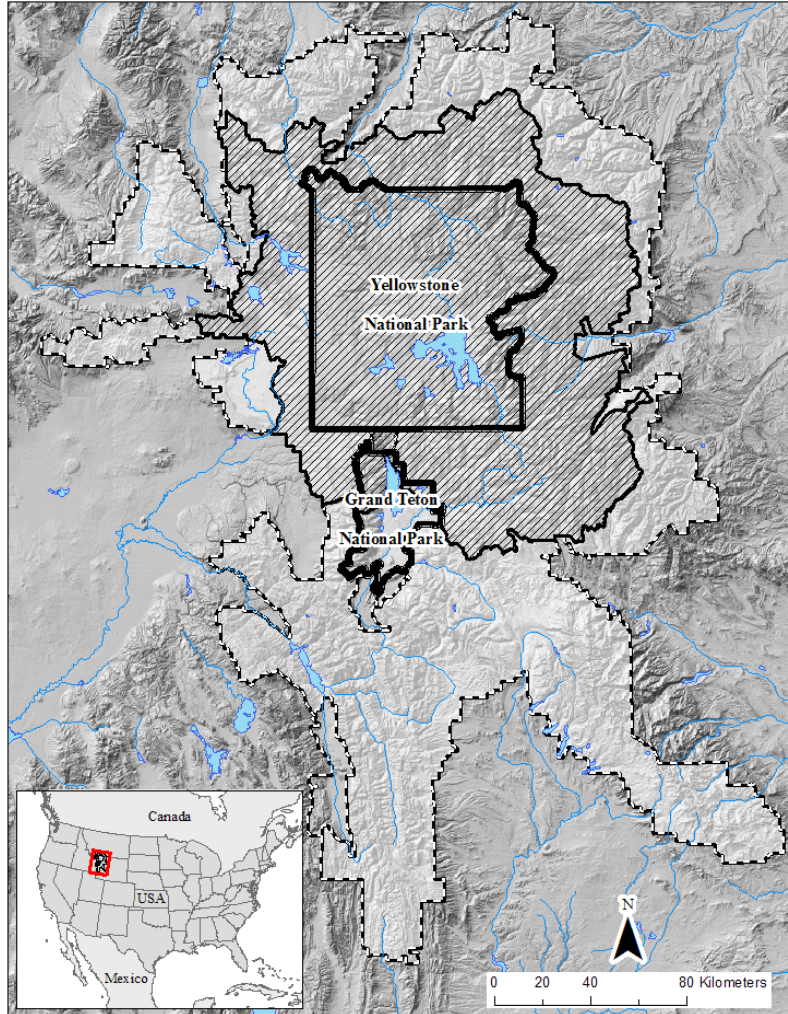


Figure 4. The Greater Yellowstone Ecosystem including Yellowstone and Grand Teton National Parks and the surrounding National Forests. The hatched area is the grizzly bear Primary Conservation Area.

influenced by the quantity and quality of available food (Stringham 1990, McLellan 1994).

Moths, at 8 kcal/g, are the richest food available to grizzly bears in the GYE (Mealey 1975, Pritchard and Robbins 1990, French *et al.* 1994). Because the moths aggregate in

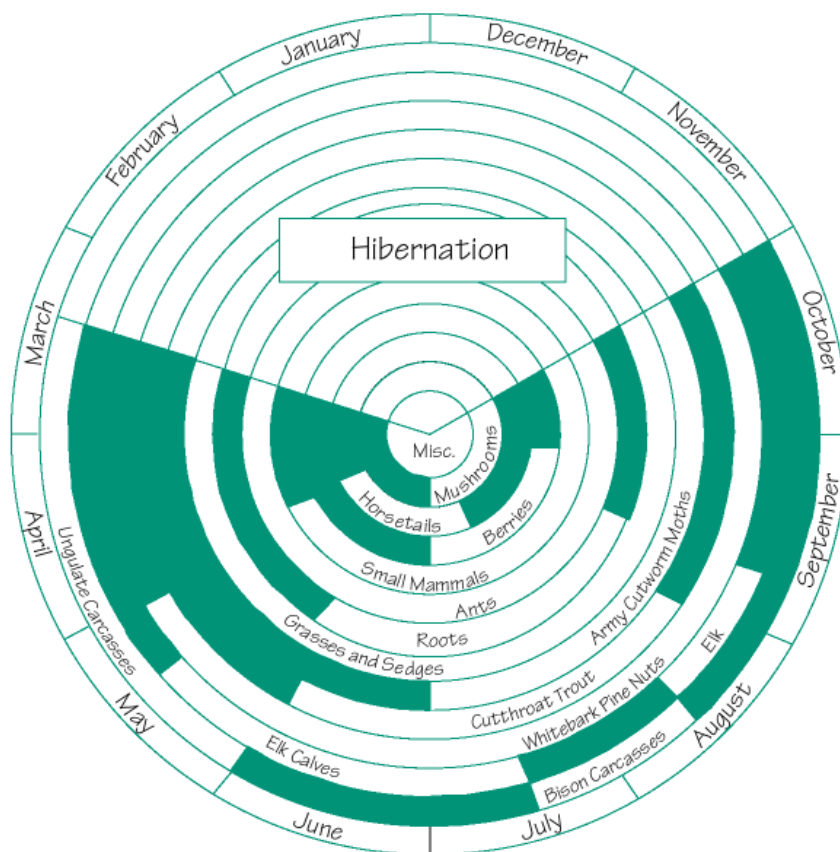


Figure 5. Seasonal availability of bear foods in the Greater Yellowstone Ecosystem (from Yellowstone National Park Bear Management Office)..

the talus they are concentrated in space and efficiently obtained by bears (French *et al.* 1994, White *et al.* 1999). Moths also are available to the bears during hyperphagia (Mattson *et al.* 1991, French *et al.* 1994) an energetically demanding time of year for bears that lasts from mid-July until denning and during which they need to accumulate fat for hibernation (Nelson *et al.* 1980).

Grizzly bears were first observed feeding on moths by scientists in the 1950s (Chapman *et al.* 1955), and outfitters in the GYE reported seeing bears forage on “moths,” “bugs”, and “insects” in high elevation talus (French *et al.* 1994). Grizzly bears

excavate the moths from their daytime hiding spots in talus and consume them by the millions from July through September (French *et al.* 1994, White 1996, White *et al.* 1998b, 1999). A grizzly bear can consume 40-60,000 moths in a day, and over a 30-day period a grizzly bear feeding extensively on moths can consume close to half of its yearly energy needs (White 1996, White *et al.* 1999). While foraging for moths bears wander the talus with their noses hovering above the rocks (French *et al.* 1994, H. Robison, pers. observ.). Moths emit pheromone while hiding in the talus (H. Robison, pers. observ.) and bears may locate moths by smell (French *et al.* 1994). Upon finding moths, the bears dig pits and forage for several minutes (French *et al.* 1994).

While bears eat millions of moths over the summer, the impact of this predation on the moth population is unknown. Studies have estimated the density of moths in a talus slope (White *et al.* 1999), but such calculations are complicated by moths that escape census by crawling into the talus or by flying away. Additionally, moth density and distribution in the talus is likely to change over the summer as moths seek microsites within the talus (H. Robison, pers. observ.) related to meltwaters or temperature gradients within it (French *et al.* 1994, White *et al.* 1998b). The flight of moths to low elevations in fall is smaller than their flight there in the early summer (Pruess 1967), but how much of this apparent mortality is due to environmental effects (e.g., weather patterns), distributional shifts during migration, or predation is unknown.

Moth sites are ecocenters, meaning that resources are abundant and clumped in space, and bears tolerate each other at close proximity while foraging (Craighead *et al.* 1995). Fifty one grizzly bears were observed feeding on moths at different sites on a single morning, and at one site twelve bears were seen feeding at the same time (French *et al.*

1994, IGBST unpub. flight reports). In 1991 and 1992, researchers estimated ~44% of Yellowstone grizzly bears use moth sites, and ~40% of these bears are females (O'Brien and Lindzey 1994). Although these estimates may be biased high due to easy sightability (but see French *et al.* 1994) of bears while they are above tree line on moth sites, they do demonstrate that moth sites are used by many bears in the population. French *et al.* (1994) suggested that moth sites are especially important to females with dependent young because one to three distinct family groups used each site throughout a moth-feeding season.

Balancing recruitment and mortality is central to managing and conserving bears in the GYE (Schwartz *et al.* 2006). Human-caused mortality remains a key determinant of grizzly bear population growth in the Rocky Mountains (Mattson *et al.* 1996, McLellan *et al.* 1999). As of 1995, 91% of the 53 recorded adult female grizzly bear deaths were caused by humans (Weaver *et al.* 1996), and from 1983-2001 all deaths of single independent females were human-caused (Haroldson *et al.* 2006). Between 1992 and 1997 22% of human-caused bear mortalities were adult females, and 11 of these 12 bears were killed in self-defense shootings by hunters (Gunther *et al.* 1994, 1995, 1996, 1997). Security from human disturbance and potential human-bear conflicts is important both to female grizzly bear survivorship and reproduction and to the resilience and persistence of grizzly bears in the Rocky Mountains (Weaver *et al.* 1996).

Whitebark pine (*Pinus albicaulis*) produces rich seeds that also are consumed in large quantities by bears and, like moths, are available in high elevations. During years when seeds are scarce, bears forage widely for alternative food (Mattson *et al.* 1992). During years when high elevation foods are scarce bears get into more fatal conflicts with humans

than during years when they are abundant (Mattson *et al.* 1992, Gunther *et al.* 1994, 1995, 1996, 1997). Additionally, the abundance of seeds positively correlates with increased grizzly bear fecundity, lower human-caused grizzly bear mortality, and reduced numbers of management actions (*i.e.*, trappings, translocations, euthanizations, and animals sent to zoos) (Mattson *et al.* 1992, Gunther *et al.* 1994, 1995). Additionally, there is a positive relationship between whitebark pine seed abundance and litter size (Mattson *et al.* 1992). Although there are no data available to test whether this relationship also exists with moths, scientists believe moths may influence reproduction and survival of a segment of the bear population in the GYE (Schwartz *et al.* 2006). Cyclic crashes in the seed crop and damage to whitebark pine from exotic white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) (Haroldson *et al.* 2003) increase the importance of understanding the factors influencing moth presence and availability to grizzly bears. A study based on field estimates and another that used isotopes indicate that bears use alternative foods (*i.e.*, meat) when whitebark pinecone production is low (Mattson 1997, Felicetti *et al.* 2003). In the same study, isotopic signatures of moths were found not to be unique from those of other herbivores and the authors were unable to determine their relative importance to bears diets (Felicetti *et al.* 2003). It is unknown whether bears use moths more or less when other foods in the GYE are low or high in abundance.

A method has been developed to monitor whitebark pine seeds in the GYE and to forecast their availability to bears. Grizzly bear managers would like to develop a similar system for moths (Schwartz *et al.* 2006). While the moth monitoring and forecasting currently conducted in low elevations suits the needs of farmers, it falls short of the needs

of grizzly bear managers. A strategy useful for bear conservation might involve forecasting the number of moths that leave low elevations en route to high elevations where they may become bear food. It would be useful for entomologists and wildlife managers to collaborate on a system to monitor moth migration. A monitoring system such as this would require techniques from various disciplines. Currently, progress in migratory ecology is encouraging and uses techniques that span disciplines from physiology and ecology (McNiel *et al.* 1995, Gould 2008) to meteorology and includes direct (e.g. aerial nets, airplanes) and indirect (e.g. X-band radar, NEXRAD Doppler radar) methods (Westbrook 2008).

Grizzly bears whose home ranges overlap Yellowstone National Park (YNP) and other parts of the GYE make long forays to forage at moth aggregation sites in the Shoshone National Forest adjacent to the park. While the ability of populations to use habitats adjacent to parks is important to the probability of their persistence within the parks (Newmark 1995), managing mortality adjacent to parks also is important (Schwartz *et al.* 2006). Given the energy grizzly bears can obtain by feeding on moths in areas adjacent to YNP, the proportion of GYE grizzly bears that use moth sites, and the proportion of these bears that are females, the presence of moths and their availability to bears at moth aggregation sites are important to the conservation of the GYE grizzly bear population.

NEXT STEPS

The ecology of *E. auxiliaris* is unusual for a noctuid in North America. Studying its ecology has been and will continue to be challenging and will likely require the

integration of a variety of different techniques ranging from genetics to various types of modeling. In the following chapters I employ a variety of techniques to answer some of the questions that remain about moth ecology. Chapter 2 is a genetics study I designed to determine from where the moths that migrate to high elevation bear foraging sites are coming. Determining this is important because if moths are coming from specific geographical areas biologists and managers must focus low elevation studies in the areas from which the moths originate. Alternatively, moths could comprise a panmictic population, and specific low elevation areas may not be important to the relationship between bears and moths. In chapter 3 I analyzed pesticide residues to determine whether or not moths harbor chemicals they acquire from pesticide treatments in agricultural areas and estimate whether these compounds may reach physiological toxicity in or bioaccumulate in bears. Chapter 4 is a habitat modeling study in which I develop models using statistics and geographic information systems to predict high elevation habitat that might be suitable for moths and bears in the GYE. In Chapter 5 I synthesize the findings of chapters 1 through 4 and propose promising directions for understanding the ecological relationship between moths and grizzly bears.

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CHAPTER 2

Army cutworm moth population genetics and migration and implications for grizzly bear conservation

INTRODUCTION

Army cutworm moths (*Euxoa auxiliaris*) are migratory noctuid moths that are native to North America. During their one-year lifespan, they play important ecological roles both in the low elevations of the Great Plains and Intermountain West where they are agricultural pests (Seamans 1927, Pruess 1967) and in the high alpine of the Rocky Mountains where they are important food for grizzly bears (*Ursus arctos horribilis*) (Mattson *et al.* 1991, French *et al.* 1994, White *et al.* 1999).

E. auxiliaris ranges from Kansas to California and from central Canada to New Mexico (Burton *et al.* 1980) (Figure 1, Chapter 1). Its geographic distribution falls within historic grizzly bear range and encompasses the current range of remaining bear populations (Burton *et al.* 1980, Servheen 1990).

The moths oviposit in soil at low elevations and the larvae over-winter underground. In the spring, the larvae surface and begin feeding on emerging crops and native plants. Once they are mature, the larvae burrow underground into cells where they pupate (Burton *et al.* 1980). The moth is prone to outbreaks; outbreaks have been attributed to climatic factors (Seamans 1927, Morrill and Jensen 1982). Although the moth is considered an infrequent pest (Jacobson and Blakeley 1959) because cereal grains can withstand a considerable amount of defoliation without measurable yield loss (Morrill

and Jensen 1982), it has been known to cause serious losses in Alberta, Montana, and Colorado (Seamans 1927). The damage it incurs can be significant economically, causing up to tens of millions of dollars in crop damage per year in some states like Montana (Rizzo 2000). When larvae reach numbers that portend decreased crop yields (Blodgett *et al.* 2003), farmers control outbreaks of larvae with various carbamate, organophosphate, pyrethroid, and organochlorine pesticides (Robison *et al.* 2006).

The moths emerge in late June and migrate hundreds of kilometers to alpine areas (elevation of 2,768 – 3,680 m) in the Rocky Mountains. The moths' migration is thought to be driven by their need to escape high temperatures at low elevations (Jacobson and Blakely 1959, Hardwick 1970), food requirements (Pruess 1967), or by an interplay between temperature and aridity in lowland habitat (Oku 1983).

The moths fly at night, fly low to the ground, and feed on nectar while en route to the mountains (Cook 1930, Pepper 1932, Pruess 1967, Lavigne 1976, Kevan and Kendall 1997). Unfavorable winds decrease the numbers of moths flying and their flight height, but do not influence their flight direction (Pruess and Pruess 1971). Oku (1983) reasoned that seasonal travel between winter and summer habitats separated by considerable distances could not have evolved without some degree of favorable winds. He also suggested that migrants fly to the nearest suitable summering sites (Oku 1983). Pruess (1967) suggested that if the moths in the mountains came from low elevations nearby, this would lead to genetic and morphological differences (*i.e.*, clines) between moths collected in the eastern versus the western portion of their range. However, Pruess (1967) did not detect clines in morphological characters. Pruess (1967) also found that moths at some high elevation sites might not have come from local populations in low

elevations. Byers *et al.* (1987) suggested that the moths may not always return to the areas of their origin based on the lack of consistency between trap catches and trap locations during two out of five years. Studies on the actual distances moved by the moths, however, have not been conducted (Hardwick and Lefkovitch 1971).

While in the mountains, the moths feed on flower nectar at night and aggregate in rock slides (*i.e.*, talus) during the day (Kevan and Kendall 1997, French *et al.* 1994, O'Brien and Lindzey 1994, White *et al.* 1998a,b, White *et al.* 1999). The moths convert the nectar they consume into lipid, and they store it in their abdomens (Kevan and Kendall 1997, French *et al.* 1994, White *et al.* 1998a, b). Starting in late August and continuing through October, the moths migrate back to low elevations (Pruess 1967).

While the moths are hiding in the talus, grizzly bears excavate them and consume them in the millions from July through September (Mattson *et al.* 1991, French *et al.* 1994, White *et al.* 1998a,b, White *et al.* 1999). When compared with other foods, moths, at 8 kcal/g, are the richest food available to grizzly bears in the Greater Yellowstone Ecosystem (GYE) (Mealey 1975, Pritchard and Robbins 1990, French *et al.* 1994). By late summer, lipids comprise 70-83% of the moths' body mass and each moth contains about 0.5 kcal (Kevan and Kendall 1997, White *et al.* 1999). Bears can eat 40-60,000 moths/day (White *et al.* 1999). In 30 days of feeding extensively on moths, a bear can consume close to half of its yearly energy needs (Sizemore 1980, White 1996).

Grizzly bears in the lower 48 states of the U.S.A. were listed as threatened under the U.S. Endangered Species Act in 1975 (USFWS 1993). Due to the success of conservation efforts, the bear population in the GYE was delisted in 2008 (USFWS 2007). In response to a legal challenge, a judge in Montana ruled in 2009 that the bear

should be relisted (USFWS 2009). Human-caused bear mortality prompted the listing of the bear (Mattson *et al.* 1996), and balancing recruitment and mortality is the key to bear conservation in the GYE (Schwartz *et al.* 2006). The balance between recruitment and mortality is, in part, influenced by two high-fat foods available at high elevations, whitebark pine (*Pinus albicaulis*) seeds and moths. When these foods are scarce, bears forage widely and get into more fatal conflicts with humans than during years when these foods are abundant (Mattson *et al.* 1992, Gunther *et al.* 1994, 1995, 1996, 1997).

Human-caused bear mortality is the major cause of death of bears in the GYE and most of these deaths occur in the autumn (Haroldson *et al.* 2006). Additionally, some females fail to produce litters when important autumn foods fail during the year of breeding (Schwartz *et al.* 2006). Furthermore, the abundance of whitebark pine seeds during the year of breeding positively influences the litter size of bears the following year (Mattson *et al.* 1992, Schwartz *et al.* 2006). While no data exist to test whether moths are important in a similar way, there is concern they could be and there is interest in better understanding moth migration and moth availability to bears (Schwartz *et al.* 2006). One study estimates that up to forty percent of Yellowstone grizzly bears feed on moths at aggregation sites (O'Brien and Lindzey 1994), and two studies suggest moths may be especially important to female bears (O'Brien and Lindzey 1994, French *et al.* 1994).

Although studies have determined that moths are important to grizzly bears in the Rocky Mountains, studies of moth and of bear ecology have been conducted largely independently and studies that link their ecologies are scarce. Better understanding gene flow in moths and moth migration is important to better understanding the ecological relationship between moths and bears and relevant to conserving bears. For example, in

some years bears use a smaller subset of all known moth sites than in other years, the cause of this is unknown, but it is inferred that the moths are not present (*i.e.*, they are not available to bears) (Bjornlie and Haroldson 2008). Understanding the factors that influence moth availability to bears involves understanding where the moths are migrating from and what influences moth abundance in their origins, en route to the mountains, and in the mountains. Thus the goal of this study was to determine whether the moths that become food for bears are panmictic or whether they comprise genetically distinct subpopulations based on their origins. If the moths come from various subpopulations, pressures in their habitats of origin (*e.g.*, pesticide use, habitat conversion, changing climate) may influence their availability to bears. Additionally, weather patterns between the specific low elevation origins of the moths and the moths' over-summering sites could influence moth abundance at high elevations. Alternatively, moths could be panmictic. In this case, conditions in specific low elevation sites might not be critical to the persistence of the ecological relationship between grizzly bears and moths, and ecological factors at a larger scale might be more important to determining their availability to bears.

Aside from elucidating aspects of moth gene flow and migration that are important to the relationship between bears and moths, there are basic questions surrounding the moth's migration and taxonomy. Because female moths are burdened with eggs during migration while males are not (Koerwitz and Pruess 1964), one might expect differences in the dispersal of males and females en route to the plains. Hence, I tested whether dispersal was biased between male and females, with the expectation that there would not be a difference between the sexes. I also I tested for genetic differences among several

color morphs described for the moths. Five forms have been described for *E. auxiliaris*: *E. auxiliaris*, *E. introferens*, *E. agrestis*, *E. montanus*, and a melanic form (Pruess 1967) (Figure 2, Chapter 1). Three of these, *E. auxiliaris*, *E. introferens*, and *E. agrestis* were discussed by Strickland (1916) and were first described as distinct species. Pruess (1967) found the only morphological characters that differed significantly between these forms were size and weight. My study could lend genetic support to the conclusion accepted currently based on morphology that these color morphs are forms of one species.

METHODS

Sampling

During summer and autumn, 2001, I collected moths from four high elevation (2900 - 3600 m) sites in Wyoming where grizzly bears feed on moths. I visited one site six times over the summer and autumn to investigate whether there was a temporal component to moth population structure. I also collected moths from 29 low elevation (1180 - 1980 m) areas in Idaho, Montana, Nebraska, and Wyoming in the autumn of 2001, circumscribing a 360 degree radius around the high elevation sampling locations (Table 1, Figure 1). I also obtained moths from a high elevation site used by black bears in New Mexico in 1999; I analyzed these samples to help determine if geographic distance has resulted in genetic isolation of moths or if moths are panmictic throughout their range. I captured moths in black-light traps or by hand at high elevations and in pheromone traps at low elevations. I preserved samples in 95% ethanol and stored them at -20° or -80° C. I keyed moths to species by dissection and inspection of reproductive structures (Lafontaine 1987).

Microsatellite analysis

I extracted DNA from the thoracic muscle of moths using Qiagen DNeasy 96 Tissue kits (Qiagen, Valencia, CA, USA) following Qiagen's protocol. For each sample, I used twenty ng of DNA to perform polymerase chain reactions (PCRs) at eleven loci using the methods described in Robison *et al.* (in prep.). I analyzed the PCR products using an ABI 3700 (Applied Biosystems, Foster City, CA, USA) machine. I genotyped the PCR products in comparison with LIZ 500 bp size standard (Applied Biosystems) using GeneMapper software (GeneMapper version 3.0, Applied Biosystems).

Data analysis

I used the programs F_{STAT} 2.9.3 (Goudet 2001), ARLEQUIN 3.11 (Excoffier *et al.* 2006), and GENEPOP (web version, Raymond and Rousset 1995) to estimate the number of alleles per locus, allelic richness, observed (H_o) and expected heterozygosities (H_E), and within group gene diversity. I also used these programs to test for linkage disequilibrium (LD) between all pairs of loci and for deviations from Hardy-Weinberg expectations (HWE). I used the program MICRO-CHECKER to test for genotyping errors caused by allelic dropout and stuttering and to detect null alleles. If null alleles are present, MICRO-CHECKER estimates their frequency (N_a) (Oosterhout *et al.* 2004).

I investigated moth population differentiation and structure using F -statistics in F_{STAT} and STRUCTURE (Pritchard *et al.* 2000). I used F_{STAT} to calculate F_{ST} , which describes the genetic variation residing among populations; F_{IS} , which describes how well genotype frequencies within populations adhere to HWE; and significance tests for both of these

measures. I used STRUCTURE to investigate whether moths collected across locations assigned to populations (k). STRUCTURE uses a Bayesian clustering approach to define populations based on allele frequency distributions that satisfy the assumptions of HWE and assigns individuals to these populations on the basis of their multilocus genotypes. STRUCTURE also generates q , each individual's proportional membership (*i.e.*, assignment) to each of the k populations. I ran the program over a range of k , compared the log probability of the data under each k (*i.e.*, $\ln[\Pr(X | k)]$), and selected the k with the highest value of $\Pr(X|k)$. I chose an admixed ancestry model, where individuals may have mixed ancestry, and correlated frequencies, where allele frequencies in the different populations may be fairly similar. I specified a burn-in period of 180,000 and performed 50,000 Markov Chain Monte Carlo (MCMC) replications after the burn-in period. I also performed a MANOVA among mean proportional assignment of individuals to populations generated by STRUCTURE to identify potential differences among moths collected in high and low elevations east and west of the Continental Divide as well as potential differences among all locations.

Sex-biased dispersal

To investigate whether moth dispersal is biased between the sexes, I analyzed a subset of eight sampling locations. This subset consisted of locations where the samples included more equal numbers of males and females. I tested for sex-biased dispersal using the *Biased dispersal* function in F_{STAT} 2.9.3 (1000 permutations) (Goudet 2001). I specified a two-tailed test because I made no *a priori* assumption about which sex might disperse most (Goudet 2002). The function generated statistics including the following:

F_{ST} , F_{IS} , H_o , H_s , and the mean and variance of AIC , which is the Assignment Index corrected for different levels of gene diversity in different populations. Although H_o is not expected to differ with dispersal status, H_s should be largest for the group dispersing most, F_{ST} will be higher for the more philopatric sex than the dispersing sex, and F_{IS} will be higher in the dispersing sex (Goudet *et al.* 2002). AIC is the probability for each individual in each location that its genotype (P) at a given locus appears there as the squared frequency of the allele p , (p^2) if it is homozygous or twice the product of the frequencies of its two alleles ($2pq$) if it is heterozygous. The most dispersing sex will include both residents with common genotypes and immigrants with rare genotypes and, therefore, is expected to be the sex with the lower AIC (Goudet *et al.* 2002). The *Biased dispersal* function assumes generations are non-overlapping, dispersal occurs prior to reproduction, and individuals are sampled post-dispersal.

Color morphs

Whenever I was able to discern the color morph of a moth (*i.e.*, their wings were not too heavily damaged), I indicated the color morph on its collection vial. I used F_{STAT} and STRUCTURE to investigate whether the color morphs reflected unique groupings based on genetic data (Goudet 2001). For analysis of these data in STRUCTURE, I specified admixed ancestry, correlated frequencies, a burn-in period of 150,000 and performed 30,000 MCMC replications after the burn-in period.

RESULTS

Sampling

A total of 1294 moths were collected for this analysis. Of these, $n=973$ were from low elevation and $n=321$ were from high elevation sites (Table 1). Thirty seven moths were collected from the high elevation site used by bears in New Mexico.

Microsatellite variability

I scored a total of 254 alleles at 11 loci for 1331 moths collected from 34 locations. Allelic diversity across all locations ranged from 6.70 to 9.18 averaged over all loci, and observed heterozygosities ranged from 0.369 to 0.557 (Table 1). Loci *Eaux4* and *Eaux11*, both with 16 alleles, had the fewest number of alleles and locus *Eaux5*, with 48 alleles, had the largest number of alleles (Table 2). All loci had instances where the repeat length did not fit the expected pattern based on the motif, which indicated the presence of insertion-deletions.

Hardy-Weinberg and null alleles

All 34 locations had at least four, and some locations had up to nine, loci out of HWE (ARLEQUIN). Locus per population tests showed heterozygote deficiency (positive F_{IS}) and departure from HWE at six (*Eaux4*, *Eaux2*, *Eaux3*, *Eaux5*, *Eaux8*, *Eaux7*) of 11 loci (F_{STAT} 2.9.3, ARLEQUIN), suggesting a pervasive influence on heterozygosity.

Analysis of the presence and frequency of null alleles in MICRO-CHECKER at each locus across locations ranged from 0.0033 at *Eaux1* to 0.3233 at *Eaux8* (Table 2, Table 3). MICRO-CHECKER analyses indicated there were no issues with stutter or allelic

dropout any loci, except perhaps for stuttering at locus *Eaux5*. Due to the pervasive heterozygote deficit and the relatively higher frequency of null alleles found at loci *Eaux4*, *Eaux2*, *Eaux3*, *Eaux5*, *Eaux8*, *Eaux7* as opposed to the other five, these six loci were excluded from further analyses. Of the remaining five loci, only a subset, *Eaux1*, *Eaux10*, and *Eaux11* were not significantly in LD with each other at the $p < 0.05$ and the $p < 0.00013$ table-wise levels. I continued population-level analyses and tests for sex-biased dispersal using these three loci (Table 3).

Population structure

Global G_{ST} (Nei 1987), an estimator of F_{ST} , was -0.002. Tests of pair-wise differentiation among sampling locations in F_{STAT} were not significant for any population pairs at the Bonferroni-adjusted 5% nominal level for multiple comparisons where significant differences are determined by $p < 0.000064$ (15600 permutations).

STRUCTURE assigned moths from the 34 sampling locations, one which was sampled six times, to three clusters (k) (Figure 2, Table 4). The highest value of $\ln[\Pr(X | k)]$ was -7107.8. The small amount of variance in $\ln[\Pr(X | k)]$ across the different runs (3-5 iterations) indicated the burn-in period of 180,000 was appropriate and the MCMC chain had converged by 50,000 iterations. MANOVA of the mean proportional assignment of individuals to the three populations generated by STRUCTURE did not support significant differences within the one location sampled over time or among sampling locations based on their elevation, their location east or west of the Continental Divide, or overall sites ($p > 0.05$ for all variables).

Sex-biased dispersal

Results from F_{STAT} indicate that males and females from the eight sampling locations disperse in the same proportions. If one sex was dispersing more than another, one would expect the sex with the higher dispersal rate to have larger within group gene diversity (H_s), lower F_{ST} , higher F_{IS} , lower mean AIC , and larger $vAIC$ than the sex with the lower dispersal rate. The values of each of these metrics were similar for both sexes and the significance tests for each of these metrics between the sexes were not significant ($p > 0.05$, 1000 permutations) (Table 5).

Color morphs

Because neither STRUCTURE nor F_{STAT} supported population differentiation, I lumped the data by color morph across all populations. There were a sufficient number of individuals to test for differences among three of the five different color morphs exhibited by the species (*E. montanus* [$n=48$], *E. introferens* [$n=42$], *E. auxiliaris* [$n=243$]). The patterns of heterozygote deficit at the 11 loci across color morphs and the LD relationships among these loci were different from those in the population-level and sex-biased analysis. Thus, for this analysis I used loci *Eaux4*, *Eaux10*, and *Eaux11*, which did not show pervasive heterozygote deficiency across populations and were not in LD with each other.

I found no significant genetic differences among the three color morphs at the Bonferroni-corrected 5% significance level ($p > 0.016$, 60 permutations). The highest value of $\ln[\text{Pr}(X | k)]$ was -1762.87. The low variance in $\ln[\text{Pr}(X | k)]$ across the different runs (3 iterations) indicated the burn-in period of 150,000 was appropriate and the

MCMC chain had converged by 30,000 iterations. Moths were assigned to three clusters (k) (Figure 3, Table 6). The mean proportional membership of each color morph to each cluster was similar, however, indicating no difference between the color morphs.

DISCUSSION

Two issues must be considered when interpreting these results. The first issue is the unusual properties of microsatellites in Lepidoptera. The second issue is aspects of the life history of *E. auxiliaris*, *i.e.*, migration, onset of mating, and the occurrence of outbreaks of the species.

Microsatellites in Lepidoptera have curious properties – they are difficult to isolate (Zhang 2004); they can exist as microsatellite DNA families with similar to identical flanking regions for different loci (Zhang 2004); and they appear to have higher frequencies of null alleles than other taxa (Endersby *et al.* 2006; Megléczy and Solignac 1998; Keyghobadi *et al.* 1999; Ji *et al.* 2003). During this study, I designed and tested 262 microsatellite primer pairs for *E. auxiliaris* and yielded 14 polymorphic loci suitable for population analyses (H. Robison, in prep.), a 5% success rate. One of my four microsatellite libraries, a –TACA library, contained microsatellite DNA families with the result that different loci isolated from this library had identical or very similar flanking regions (H. Robison, unpub. data). Once I detected this issue, I abandoned this library as a source for generating loci.

Some alleles may not amplify in PCR when mutations have occurred at locus priming sites – these unamplified alleles are called null alleles (Shaw *et al.* 1999, Wagner *et al.* 2006). Null alleles cause false homozygotes and lower the levels of polymorphism

observed at loci. The power of genetic tests is influenced by the level of polymorphism of the loci that are used. Power increases when there are more alleles per locus (Goudet *et al.* 2002). Null alleles can also cause deviations from Hardy-Weinberg proportions by inflating homozygote proportions at loci. These deviations from HWE can be misconstrued as assortative mating, inbreeding or Wahlund effects. Additionally, null alleles lower apparent genetic variability and, therefore, may confound population genetic analyses that rely on HWE (Pritchard *et al.* 2000) and may inflate estimates of genetic differentiation incorrectly (Chapuis and Estoup 2007, Chapuis *et al.* 2008, Carlsson 2008).

Chapuis and Estoup (2007) suggest that null alleles are likely to be found in populations with a large effective population size (N_e); *E. auxiliaris* has populations comprising millions of individuals. The eleven loci used in this study contained null alleles ranging in average frequency from 0.003 to 0.323 for each locus across all populations (Table 2). Hence, to avoid spurious inferences of population structure, the 6 loci that both displayed heterozygote deficiency across all populations and contained high levels of null alleles were excluded from this analysis. Of the remaining 5 loci, two were in LD with each other; this left three loci with which I could analyze population structure in *E. auxiliaris*. It is possible that the linked loci could have been isolated from the same chromosome, of which most *Euxoa* have a haploid number of 31, or that the loci were part of a microsatellite DNA family complex.

The three loci I used for this analysis had null allele frequencies ranging from 0.003 to 0.147 across populations. The results I present here on the null allele frequencies per locus per population, the null allele frequencies averaged over loci for each population,

and the mean null allele frequency over all populations are all within the ranges of results presented in other studies (Keyghobadi *et al.* 1999, Harper *et al.* 2003, Endersby 2006, Franck *et al.* 2007, Chapuis *et al.* 2008, and Carlsson 2008) (Table 3). I chose not to correct the genetic data for *E. auxiliaris* because recent studies have addressed both the affects of null alleles on metrics of population genetics and the adjustments of these measures for null alleles (Chapuis and Estoup 2007, Chapuis *et al.* 2008, Carlsson 2008), and at least one study has shown the effects of null alleles are slight, although significant, on some methods (Carlsson 2008). Chapuis and colleagues (2008, 2007) found that including null alleles (INA) by applying a new allele size to each null allele across all populations partially fixed bias in the number of alleles and H_O but continued to underestimate their values. INA also positively biased F_{ST} and resulted in lower estimates of H_E and R_S (corrected allelic diversity) than were found with uncorrected datasets (Chapuis *et al.* 2008). Chapuis and colleagues (2007, 2008) found the method they proposed called ENA, excluding null alleles, in which they calculate F_{ST} from datasets corrected for null alleles but limit the calculation to visible allele sizes, corrects the positive bias on F_{ST} caused by null alleles.

A recent study (Carlsson 2008) indicated that adjusting for null alleles may not be necessary and other studies (Chapuis *et al.* 2008) have used uncorrected data to achieve more parsimonious results. Using simulated data, Carlsson (2008) found that null alleles only slightly (+0.003 – 0.004 units), although significantly, biased F_{ST} , and that bias in F_{ST} increased as its value became higher. Carlsson (2008) also modeled the effects of null alleles on the efficacy of assignment tests and found that even though some populations had null allele frequencies of up to 0.913 at a single locus, null alleles only

slightly (0.2 to 2.4 percent units), although significantly, reduced the proportion of correctly assigned individuals in both STRUCTURE and GENECLASS. Carlsson (2008) found that both the number of loci and the level of genetic differentiation are more influential on the accuracy of assignment than are null alleles. As one might expect, Carlsson (2008) found the proportion of correctly assigned individuals was as low as 25% at low levels of F_{ST} ; this result is consistent with the findings of other studies (Cornuet *et al.* 1999, Waples and Gaggiotti 2006).

Results from F_{STAT} do not support genetic differentiation among moth sampling locations or within the one location sampled over time, and although STRUCTURE assigned moths from all locations to three clusters, a MANOVA of the mean proportional membership of individuals within sampling locations to these clusters was not significant and was not related to position East or West of the Continental Divide or to high or low elevation. When explaining distribution of species of *Euxoa* in western North America, Hardwick and Lefkovitch (1971) surmised that the Rocky Mountains are not likely to be a barrier to *Euxoa* species because species composition within the genus is similar in similar habitat associations in the Great Basin and the Great Plains. The results I report here suggest the proportional memberships of individuals to the three clusters generated by STRUCTURE were likely arbitrary and support the idea that at least one species of *Euxoa*, *E. auxiliaris*, can disperse across the Rocky Mountains. These results indicate that at the population level the moths sampled in this study are panmictic or nearly so. STRUCTURE and other non-*a priori* assignment methods have a low percentage of correct assignment under high levels of gene flow (Waples and Gaggiotti 2006). Pritchard *et al.* (2000) and Falush *et al.* (2003) admit STRUCTURE's estimation of the number of

populations (k) is an *ad hoc* procedure and recommend that k be used only as a guide, and Waples and Gaggiotti (2006) suggest interpreting k with caution for species with high dispersal abilities.

E. auxiliaris is a highly vagile species and is known to migrate up to 300 km in 65 hours and up to 214 km in a single flight, with flights up to 80 km not uncommon (Koerwitz and Pruess 1964). One might expect substantial gene flow under this scenario; however, some specifics of the reproductive ecology of the moths remained unknown. It was thought that the moths aestivated in the summer (Pepper 1932, Jacobson and Blakely 1959, Burton *et al.* 1980). Subsequent work found that the moths do not aestivate (Kendall *et al.* 1981, Kevan and Kendall 1997), but rather migrate to high elevations, feed on nectar, and accumulate abdominal fat over the summer (Pruess 1967, Kevan and Kendall 1997). Some researchers have asserted that little or no reproduction occurs with *E. auxiliaris* in alpine areas (Pruess 1967, White *et al.* 1998a, Kevan and Kendall 1997) and that the moths mate and lay eggs upon returning to plains (Pruess 1967, Pruess and Pruess 1971, Morrill and Jensen 1982, Oku 1983). By looking at the presence or absence of maturing ova in moths, Kevan and Kendall (1997) found that females and males become reproductively mature in late summer and stated that this process may start in the alpine zone. Kendall *et al.* (1981) observed one mating event of the moths in the alpine, while French *et al.* (1994) mentioned occasional mating events and believed that a significant amount of mating occurs in high elevations. Observations of mating moths from a distance should be interpreted cautiously because there are other noctuid moth species that frequent high elevations and look similar to *E. auxiliaris* (Hardwick 1970). None of these studies looked for spermatophores in the corpus bursae of females

collected in high elevations. I observed hundreds of moths mating in the talus in the late evening late in the summer, keyed them to species, and inspected them for spermatophores (H. Robison, in prep.). These observations show that females collected in high and low elevations contain spermatophores and that eggs mature over the summer. These findings indicate that moths begin mating in high elevations and finish mating in low elevations.

The results from F_{STAT} indicate there is no bias in dispersal between *E. auxiliaris* males and females. This makes sense given that high temperatures and aridity in low elevations during the summer are similar for both males and females. Also, both sexes develop fat bodies in the alpine (Kevan and Kendall 1997), migrate (Oku 1983), and presumably use this fat body to fuel their migration back to low elevations (White *et al.* 1998). Koerwitz and Pruess (1964) found that although egg development and oviposition impose some limitations on flight ability, moths still can fly until they have finished ovipositing. Females with diminishing fat bodies and numbers of eggs continued to fly between 23 and 94 km in a single flight (Koerwitz and Pruess 1964). Hence, females may oviposit over a range of suitable habitats as they return to low elevations.

Genetic analyses of three color morphs of *E. auxiliaris*, *E. auxiliaris*, *E. introferens*, and *E. agrestis*, which were first described as distinct species but later attributed to within species variation (Hardwick 1970), support the latter interpretation.

Population genetics studies of moth pests have included allozymes (Pashley *et al.* 1985, Korman *et al.* 1993), mitochondrial DNA (Margaritopoulos *et al.* 2007, Coates *et al.* 2004), RAPD analysis (Zhou *et al.* 2000, De La Pozza *et al.* 2008) and, much less commonly, microsatellites (Scott *et al.* 2005a, Scott *et al.* 2005b, Endersby *et al.* 2006,

2007, Frank *et al.* 2007). The results I report here from Structure and analyses of F_{ST} based on variation at microsatellites indicate that high levels of gene flow occur within *E. auxiliaris* in the Great Plains and Intermountain West. Global F_{ST} was very low (-0.002), and pairwise tests between sampling locations also were very low and not significant. The time and scale over which the moths mate evidently result in panmixia or at least extremely high gene flow. My findings are consistent with those of population genetic studies of other lepidopteran pests that are dispersive or migratory that also have found low genetic differentiation among populations (Korman *et al.* 1993, Zhou *et al.* 2000, Franck *et al.* 2007, Endersby *et al.* 2006, 2007).

Microsatellite analyses of another noctuid moth, *Plutella xylostella*, that disperses hundreds of kilometers or more found no evidence of genetic structure among samples from different locations and times within Australia nor from specimens collected in New Zealand ($F_{ST} = 0.002 - 0.0051$) (Endersby *et al.* 2006, 2007). Studies of *Cydia pomonella*, a Tortricid moth that disperses up to 25 km, included samples taken in France, Italy, Armenia, and Chile and found no difference between specimens collected throughout France ($F_{ST} = 0.006$) and little difference between countries ($F_{ST} = 0.066$) (Franck *et al.* 2007). *Helicoverpa armigera*, another noctuid moth, flies as far as 1000 km, and a RAPD analysis found very low (0.011), although significant, values of θ (an estimator of F_{ST}) across populations in Israel and Turkey and lower levels among Turkish and Israeli populations ($\theta = 0.004$), indicating high levels of gene flow (Zhou *et al.* 2000). This study also found that although there was high gene flow over large geographic areas, the effects of topography influenced the moth's genetic structure (Zhou *et al.* 2000). Although I tested for the effects of topography, moths collected from

different sides of large barriers (*e.g.*, the Absaroka Mountains and Teton Mountains) and over large spatial scales, New Mexico to northern Montana, did not show genetic differences or assign to different clusters. This finding is consistent with the description of their ecology that the Rocky Mountains are not likely a barrier to the moths (Hardwick and Lefkovitch 1971).

Additionally, the population dynamics of outbreaks may decrease differences among populations (Chapuis *et al.* 2008) and decrease any effects of genetic drift. As has been found with other outbreaking species (Chapuis *et al.* 2008), the lack of divergence of *E. auxiliaris* at these neutral loci might result from demographic flushes and the decreased effect of genetic drift in the resultant large populations. Zhang (2004) suggests the characteristics of microsatellites in Lepidoptera (*i.e.*, low frequency in the genome but high redundancy with relatively few existing as single-copy sequences) imply that microsatellites are in an early stage of evolution in this order of insects, and a large proportion of them likely have experienced recent propagation or multiplication in the genome. Hardwick (1970) also points out that the genus *Euxoa* seems to be in “a state of great evolutionary mutability,” and because of this he states that the genus is a very difficult one in which to work. These properties, coupled with the tendency to migrate and outbreak, very likely influence the low levels of differentiation within this species.

Implications for grizzly bear conservation

The finding that *E. auxiliaris* moths that migrate to high elevations do not comprise unique subpopulations is important both to the persistence of the ecological relationship between grizzly bears and the moths and to grizzly bear conservation in the Rocky

Mountains. Bear conservation is facilitated when bears, seeking lipid-rich foods like whitebark pine seeds and moths, use remote, high elevation habitats that are relatively secure from conflicts with humans. High gene flow among moth populations suggests that local perturbations in one or subset of the moths' winter habitats (*e.g.*, pesticide use, habitat conversion) will not result in the moths' absence from specific high elevation sites. Significant population structure, indicative of site fidelity, would make the moths highly susceptible to local perturbations at low elevations and likely result in corresponding extirpations at high elevation sites. Previous studies show that *E. auxiliaris* flies westward to the Rocky Mountains from the Great Plains and Intermountain West in early late spring/early summer (Pruess 1967, Pruess and Pruess 1971). The results of this study indicate that the moths are panmictic or nearly so, and this suggests that the moths also may migrate eastward toward the Rocky Mountains from the west.

On a larger scale, changing climate on a regional level may influence migration of *E. auxiliaris*. First, the moths are found close to the top of high peaks in the Rocky Mountains. As climate warms, this could affect the distribution and availability of the nectar sources upon which moths rely to accumulate their fat stores for migration. Additionally, a warming climate could affect the snowpack and the microsites the moths use within the talus (French *et al.* 1994, White *et al.* 1999, H. Robison pers. observ.), and suitable habitat may disappear except at the highest elevations. *E. auxiliaris* migration is more pronounced – it starts earlier in the summer and ends later in the autumn – in the southern part of its range (30-40° latitude), than in the northern part of it (40-50° N) and ceases altogether N of 50° (Hardwick and Lefkovitch 1971, Oku 1983). This may be

why observations of grizzly bears feeding on moths have not been documented North of Glacier National Park.

Understanding the availability of *E. auxiliaris* to grizzly bears is complicated by the remote and rugged character of the moths' high elevation habitat, the huge geographic expanse of their low elevation habitat, and the scale over which their migration occurs. Managers, instead of designing moth inventories in localized areas to estimate the availability of moths to bears, need to focus on broader-scale sampling protocols in low elevations adjacent to sites used by bears. Fortunately for bears, *E. auxiliaris* is not as damaging to crops as other agricultural pests; it usually only stunts the growth of crops and does not kill them. Farmers, therefore, accept a certain level of damage to their crops before controlling them, and the likelihood of a concerted pesticide application on a large scale that may dramatically decrease moth populations is, therefore, unlikely.

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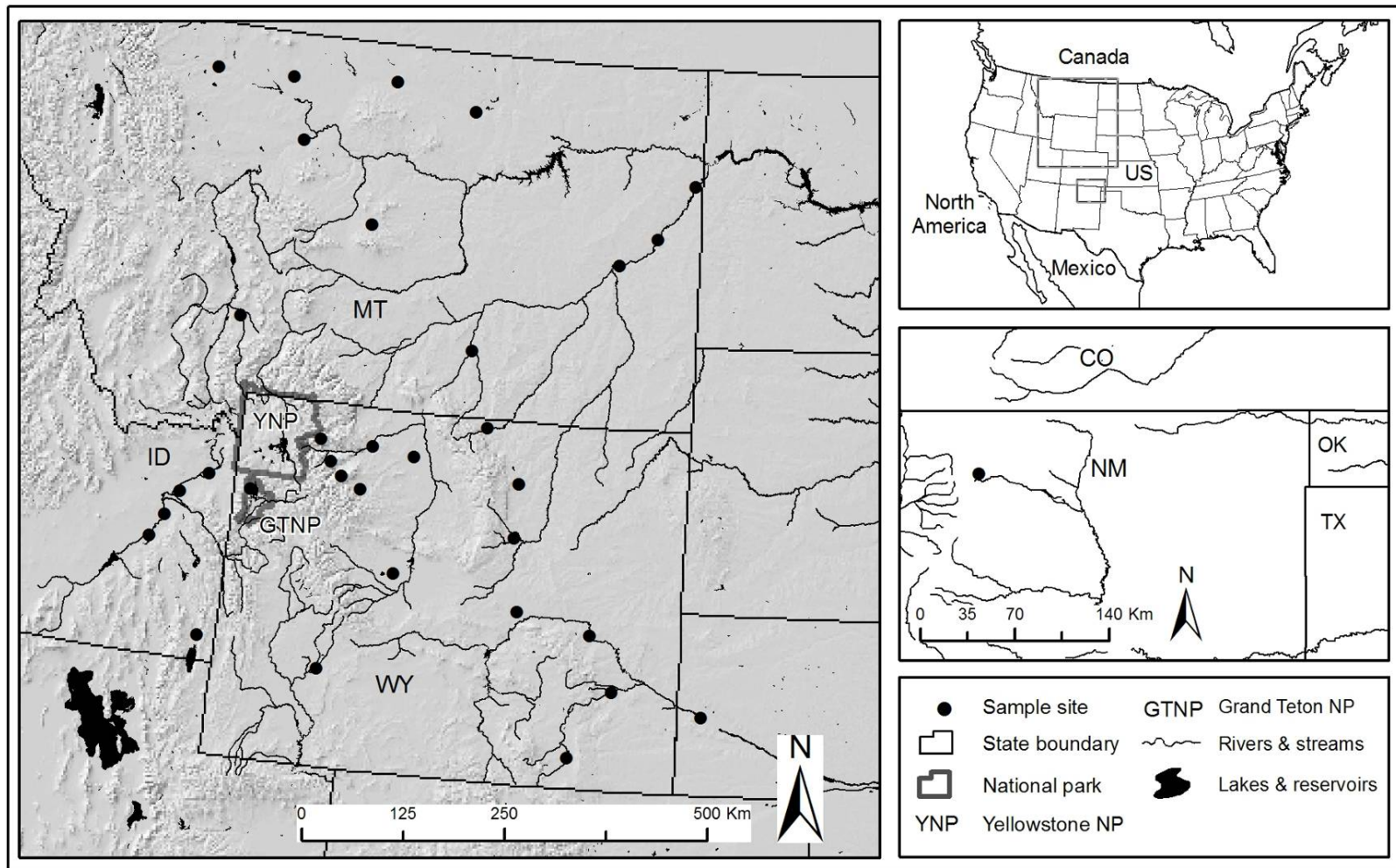


Figure 1. Sampling locations for *E. auxiliaris*.

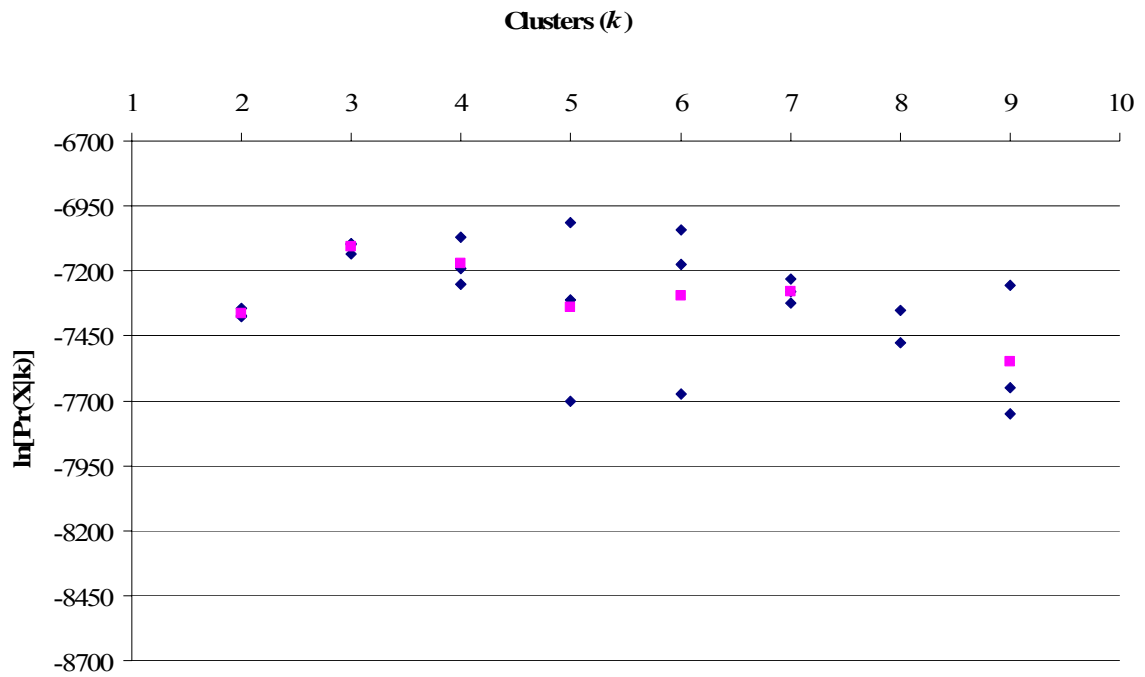


Figure 2. The negative natural log of the probability of the data, given the number of population clusters (k) estimated by STRUCTURE for *E. auxiliaris* collected from 34 sampling locations.

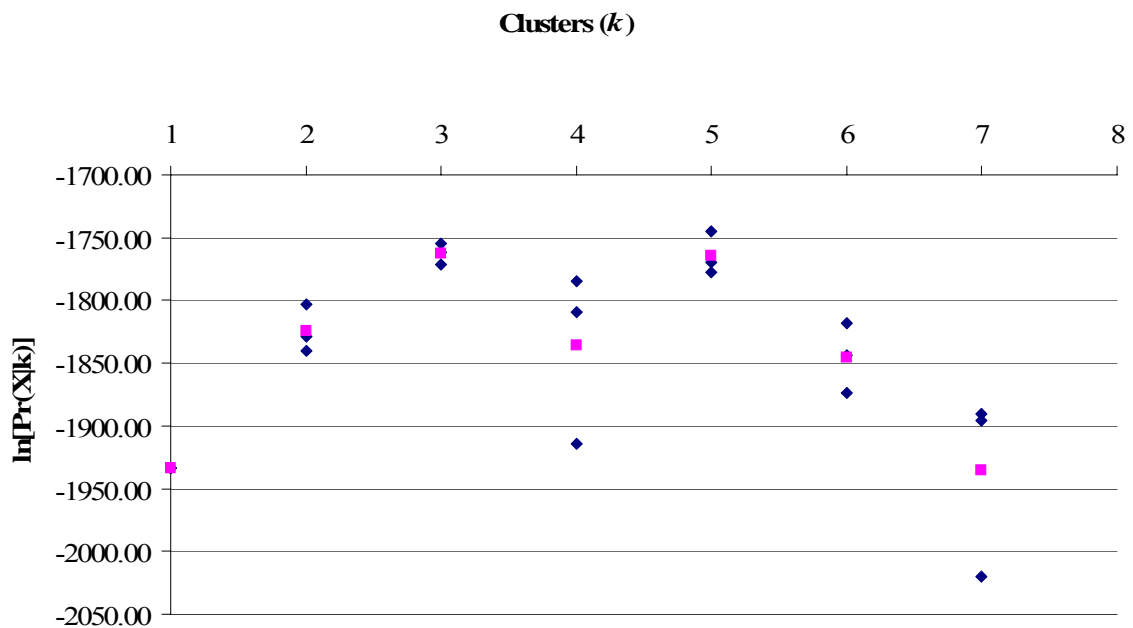


Figure 3. The negative natural log of the probability of the data, given the number of population clusters (k) estimated by STRUCTURE for three *E. auxiliaris* color morphs.

Table 1. The number of *E. auxiliaris* sampled (N), and mean values for number of alleles (a), allelic richness (r), and observed (H_O) and expected (H_E) heterozygosities, multilocus estimates of F_{IS} , and multilocus estimates of null alleles (N_a) for each sampling location.

Sampling location	N	a	r	H_O	H_E	F_{IS}	N_a
Cutbank, Glacier County, MT	27	7.273	6.770	0.462	0.671	0.316	0.128
Glendive, Dawson County, MT	33	8.273	7.680	0.432	0.702	0.389	0.181
Fort Benton, Choteau County, MT	29	7.455	7.050	0.487	0.604	0.198	0.085
Sangre De Cristo Mts., Colfax County, NM	37	8.000	7.120	0.486	0.641	0.245	0.087
Pitchfork, Park County, WY	35	8.091	7.530	0.459	0.689	0.338	0.161
Sidney, Richland County, MT	35	7.545	7.200	0.518	0.657	0.214	0.096
Scottsbluff, Scotts Bluff County, NE	38	8.636	7.870	0.440	0.666	0.343	0.175
Terry, Prairie County, MT	35	7.182	6.910	0.456	0.666	0.319	0.146
Marysville, Fremont County, ID	35	7.727	7.090	0.403	0.646	0.380	0.178
Buffalo, Johnson County, WY	35	8.000	7.560	0.497	0.653	0.243	0.112
Cody, Park County, WY	37	9.182	8.640	0.432	0.694	0.382	0.178
Dayton, Sheridan County, WY	35	8.727	8.200	0.453	0.654	0.312	0.151
Douglas, Converse County, WY ^a	35	8.500	7.190	0.494	0.669	0.265	0.123
Emblem, Big Horn County, WY	35	8.545	8.030	0.491	0.701	0.303	0.147
Eden, Sweetwater County, WY	28	6.364	5.770	0.385	0.575	0.335	0.121
Firth, Bingham County, ID	35	7.636	7.060	0.420	0.663	0.372	0.176
Kaycee, Johnson County, WY	35	7.818	5.590	0.453	0.706	0.364	0.157
Idaho Falls, Bonneville County, ID	35	9.091	8.130	0.480	0.716	0.333	0.162
Laramie, Albany County, WY	30	8.273	7.790	0.436	0.629	0.312	0.121
Malta, Phillips County, MT	30	6.727	6.420	0.399	0.664	0.404	0.200
Montpelier, Bear Lake County, ID	26	8.000	7.440	0.478	0.655	0.276	0.145
Natrona, Natrona County, WY	35	7.091	6.540	0.396	0.610	0.355	0.166
Pavillion, Fremont County, WY	35	8.364	8.090	0.405	0.610	0.339	0.149
Rexburg, Madison County, ID	35	8.091	7.530	0.484	0.661	0.272	0.124
Absaroka Mts. 1, Park County, WY	36	8.182	7.210	0.461	0.607	0.243	0.104
Absaroka Mts. 2, Park County, WY	35	6.364	4.560	0.557	0.710	0.225	0.050
Tetons Mts. 1, Teton County, WY	33	7.818	7.290	0.393	0.592	0.341	0.147
Chester, Joplin, Liberty County, MT ^b	31	6.700	3.121	0.459	0.666	0.316	0.155
Fergus County, MT	39	8.364	7.920	0.410	0.604	0.324	0.164
Gallatin County, MT	33	7.364	5.820	0.416	0.636	0.352	0.168
Carbon County, MT	33	9.000	8.670	0.399	0.626	0.367	0.176
Wheatland, Platte County, WY	35	7.455	7.220	0.522	0.678	0.234	0.081
Hardin, Big Horn County, MT	34	7.909	7.000	0.474	0.668	0.294	0.123
Absaroka Mts. 3, Park County, WY	35	7.000	6.780	0.436	0.609	0.288	0.135
Absaroka Mts. 3, Park County, WY	40	7.818	7.376	0.369	0.669	0.452	0.209
Absaroka Mts. 3, Park County, WY†	35	8.400	5.790	0.455	0.689	0.345	0.149
Absaroka Mts. 3, Park County, WY	35	7.364	6.690	0.403	0.617	0.351	0.110
Absaroka Mts. 3, Park County, WY	35	8.091	6.750	0.415	0.637	0.353	0.156
Absaroka Mts. 3, Park County, WY	37	8.364	7.990	0.380	0.671	0.438	0.188

^aresults from 10 loci

^bresults from 9 loc

Table 2. Locus name, repeat motif, number of alleles (N), size range of alleles, and null allele frequency (N_a) across all populations.

Locus	Repeat motif	N alleles	Range	N_a
Eaux1	(CAG) ₁₁	21	150-191	0.0033
Eaux2	(CAG) ₅	20	241-257	0.2264
Eaux3	(GCT) ₉	29	291-333	0.2032
Eaux4	(GCT) ₂ GCCTGT(GCT) ₆	16	223-239	0.1560
Eaux5	(CTGG) ₇	48	133-201	0.1900
Eaux6	(GCT) ₁₂	20	152-197	0.0048
Eaux7	(CAG) ₇	21	220-253	0.1483
Eaux8	(GCT) ₆	21	246-264	0.3233
Eaux9	(CAG) ₁₁	24	223-277	0.0802
Eaux10	(CAG) ₅ CA(CAG)G(CAG) ₂	18	179-200	0.1466
Eaux11	(CAG) ₅ CA(CAG)G(CAG) ₂	16	163-181	0.0816

Table 3. Estimated null allele frequencies of *Euxoa auxiliaris* and some other species.

	Robison 2009		Chapuis <i>et al.</i> 2008	Carlsson 2008	Keyghobadi <i>et al.</i> 1999	Harper <i>et al.</i> 2003	Endersby <i>et al.</i> 2006	Franck <i>et al.</i> 2007
	<i>Euxoa auxiliaris</i>		<i>Locusta migratoria</i>	Simulated data	<i>Parnassius smintheus</i>	<i>Polyommatus bellargus</i>	<i>Plutella xylostella</i>	<i>Cydia pomonella</i>
Number of loci	3	11	14	4, 12, 20	4	5	6	9
The range at a given locus among locations	0 - 0.3056	0 - 0.4567	0 - 0.753	0 - 0.913	0 - 0.360	0.03 - 0.20	*	0 - 0.55
Averaged over loci for each population	0 - 0.196	0.05 - 0.209	0.077 - 0.250	*	0.133 - 0.208	*	0 - 0.272	0.07 - 0.102
Mean frequency overall populations	0.076	0.1421	0.189	≤0.202	0.169	0.11	0.074	0.085

*not indicated

Table 4. Likelihood of the *E. auxiliaris* genetic data assuming different numbers of clusters (k) estimated by STRUCTURE.

k	$\ln[\Pr(X k)]$	$\Pr(k)$
2	-7364	4.6×10^{-112}
3	-7108	1.0
4	-7170	1.6×10^{-27}
5	-7342	2.9×10^{-102}

Table 5. Group statistics for sex-biased dispersal of *E. auxiliaris*.

	Female	Male	p value
F_{IS}	0.094	0.158	0.456
F_{ST}	-0.007	0.005	0.511
$mAIC$	0.044	-0.033	0.765
$vAIC$	3.939	4.921	0.487
H_s	0.467	0.506	0.401

Table 6. Likelihood of the genetic data from three *E. auxiliaris* color morphs assuming different numbers of clusters (k) estimated by STRUCTURE.

k	$\ln[\Pr(X k)]$	$\Pr(k)$
2	-1824	2.13×10^{-27}
3	-1763	0.438
4	-1836	6.87×10^{-33}
5	-1764	0.086
6	-1845	3.96×10^{-37}

CHAPTER 3

Assessment of pesticide residues in army cutworm moths (*Euxoa auxiliaris*) from the Greater Yellowstone Ecosystem and their potential consequences to foraging grizzly bears (*Ursus arctos horribilis*)

INTRODUCTION

Grizzly bears (*Ursus arctos horribilis*) in the lower 48 states of the USA were listed as threatened by the US Fish and Wildlife Service in 1975 (USFWS 2003), and they were proposed for delisting in November of 2005. A conservation strategy was developed to facilitate delisting, meanwhile questions remain about some key bear foods (USFWS 2003). For example, there is concern army cutworm moths (*Euxoa auxiliaris*) (ACMs) may contain pesticides that could bioaccumulate in bears (French *et al.* 1994).

ACMs are migratory noctuids native to North America. During their one-year lifespan they play important ecological roles in low elevations in the Great Plains and intermountain west as agricultural pests (Pruess 1967) and in high elevations in the Rocky Mountains as an important food for grizzly bears (Mattson *et al.* 1991; French *et al.* 1994; White *et al.* 1998b). ACMs range from Kansas to California and from central Canada to Arizona and New Mexico (Burton *et al.* 1980). Their geographic distribution falls within historic grizzly bear range, encompassing the current range of remaining bear populations (Burton *et al.* 1980; Servheen 1990).

ACMs oviposit in soil at low elevations, and larvae over-winter underground. Larvae surface in spring to feed on emergent crops and native plants, then burrow underground to pupate (Burton *et al.* 1980). Farmers control larval outbreaks with various pesticides (Table 1).

Adult moths emerge in late June and migrate hundreds of kilometers to alpine areas in the Rocky Mountains. Here they over-summer, feeding on flower nectar at night, forming large aggregations in talus during the day (Pruess 1967; Mattson *et al.* 1991; French *et al.* 1994; Kevan and Kendall 1997). While hiding in talus ACMs metabolize nectar into fat and increase their body fat up to 60% over the summer (Kevan and Kendall 1997). Grizzly bears excavate ACMs from the talus, consuming millions from July through September (Mattson *et al.* 1991; French *et al.* 1994; White *et al.* 1999).

ACMs are the richest bear food in the Greater Yellowstone Ecosystem (GYE) and are an important food during pre-hibernation hyperphagia (Pritchard and Robbins 1990; French *et al.* 1994). White *et al.* (1999) estimated a 115 kg grizzly bear could eat 40,000 ACMs day⁻¹ and >1 million month⁻¹, representing 47% of its annual caloric budget (White 1996; White *et al.* 1999). O'Brien and Lindzey (1994) estimated that approximately 45% of GYE grizzly bears used moth sites. However, this proportion is likely biased high because bears at moth sites are more conspicuous than bears in other habitats.

Long distance transport of elements and chemicals from low to high elevations has been reported for alfalfa webworm moths (*Loxostege cereralis*), Bogong moths (*Agrotis infusa*), and other insects (Halfpenny 1994; Green *et al.* 2001). Bogong moth and ACM ecology are similar. Bogong moths migrate from agricultural areas in southwestern Australia to the Snowy Mountains and the Victorian Alps. They aggregate in caves, forming the primary

food of the endangered pygmy possum (*Burramys parvus*). Bogong moths contain arsenic, which they transport from low to high elevations, and pygmy possums consume it (Green *et al.* 2001).

Because grizzly bears consume millions of ACMs, concern exists about transport of pesticides that could bioaccumulate in bears (French *et al.* 1994).

Threats of pesticides

It is well-known that potentially toxic elements and chemicals can persist in environments and bioaccumulate in organisms (Kelly *et al.* 2004). At the time of this study, carbamate, organophosphate, and pyrethroid chemicals were listed for controlling ACM larvae in the states of Idaho (ID), Montana (MT), Nebraska (NE), South Dakota (SD), and Wyoming (WY) (Table 1, Fig. 1). MT also recommended the use of two organochlorine pesticides (Table 1).

Organochlorines resist degradation and are ingested by organisms through their water and food (Schuurmann and Markert 1998). They are soluble in fat, and the amount of fat in an organism influences chemical bioconcentration (Schuurmann and Markert 1998).

Organochlorines have bioaccumulated in various species including bald eagles (*Haliaeetus leucocephalus*) (Bowerman *et al.* 1998); ringed seals (*Phoca hispida*) and polar bears (*Ursus maritimus*) (Zhu and Norstrom 1993); Western European river otters (*Lutra lutra*) (Leonards *et al.* 1997); and the food web comprising lichen (e.g., *Cladina rangiferina* and *Cetraria nivalis*), caribou (*Rangifer tarandus*), and wolves (*Canis lupus*) (Kelly and Gobas 2001).

Although some organochlorines are metabolized by most homeotherms and may not be stored in their tissues (Hoffman *et al.* 1995; Kamrin 1997), they are suspected endocrine disrupters that may alter mating behavior, reproduction (Adeoya-Osiguwa *et al.* 2003), and development (Bevan *et al.* 2003).

Carbamates, organophosphates, and pyrethroids are metabolized and excreted by most organisms and rarely bioconcentrate in food chains (Smith and Stratton 1986; Hill 1995; Kamrin 1997). However, they can alter animal behavior (Smith and Stratton 1986; Hill 1995), disrupt endocrine function (Colborn *et al.* 1993), inhibit reproduction and development (Mathur and Bhatnagar 1991; Mantovani 2002; Adeoya-Osiguwa *et al.* 2003), and have chronically toxic (Baron 1991; Kamrin 1997) and teratogenic effects (Mathur and Bhatnagar 1991; Kamrin 1997). Pyrethroids may be carcinogenic (Chen *et al.* 2002), but organophosphates and carbamates do not appear to be (Baron 1991; Kamrin 1997; Chen *et al.* 2002).

Thus, ACMs are controlled by pesticides that could potentially bioaccumulate and be physiologically toxic to bears (Kamrin 1997 and references therein) (Table 1). Consequently, we investigated the following questions: 1) do ACMs transport pesticides to high elevation grizzly bear foraging sites? 2) if so, do ACMs contain pesticide concentrations sufficient to reach physiological toxicity in grizzly bears?

METHODS AND MATERIALS

Study Area

Our study area included the Absaroka and Teton mountain ranges of northwestern WY, U.S.A. (Fig. 1). The Absaroka Range runs north to south along the eastern border of Yellowstone National Park (YNP). Elevations range from 1,830 m to 4,006 m. The Teton Range runs north to south and is bordered north by YNP, east by Jackson Hole, west by the Teton Basin, and south and southeast by the Snake River and Gros Ventre ranges, respectively. Elevations range from 2,133 m to 4,197 m (Love *et al.* 2003). Deep valleys, cirques, sharp ridges, and floodplains characterize these ranges (Smith *et al.* 1993; Sundell 1993; Love *et al.* 2003). Climate, geology, vegetation, and fauna have been described previously (Baker 1944; Patten 1963; Waddington and Wright 1974; Dirks and Martner 1982; Thilenius and Smith 1985; Despain 1990; Marston and Anderson 1991; Sundell 1993; Smith *et al.* 1993; Clark *et al.* 1999; Love *et al.* 2003).

ACMs aggregate in talus at elevations between 3,024-3,680 m located at the base of large headwalls above timberline. The talus typically contains rocks measuring 8-40 cm and lacks vegetation (Mattson *et al.* 1991). Alpine tundra and meadows are nearby and support the flowering plants on which ACMs feed.

Sampling

In 1999, we collected ACMs from each of four high elevation sites in the Absaroka Range and one site in the Teton Range (Fig. 1, see Table 2 for sample sizes). ACMs were collected from one site (Absaroka site 1) four times to evaluate potential temporal differences

in pesticide levels. We also analyzed ACMs from an aggregation site used by American black bears (*Ursus americanus*) in New Mexico (Table 2, Fig. 1). Samples were either stored in ethanol or air-dried and stored in envelopes. In 2001, we revisited Absaroka site 1 and collected additional ACMs, which were frozen shortly after collection.

Pesticide residue analyses

Gas chromatography with electron capture detection

In 1999, we screened ACMs for organochlorines, carbamates, organophosphates, and pyrethroids listed for controlling larvae in the states of ID, MT, NE, SD and WY (Table 1). Because farmers have used pesticides not recommended to control ACM larvae (e.g. diazinon [Robison, personal observation]), we also screened for additional chemicals.

ACMs were analyzed by the USGS Columbia Environmental Research Center (CERC), in Columbia, Missouri, using gas chromatography with electron capture detection (GC-ECD) (Table 1). A detailed protocol is contained in Lebo *et al.* (2000). Samples were screened for 32 chemicals comprising a standard CERC pesticide-screening panel (Table 1). Sample dialysates and procedural controls were purified by size exclusion chromatography, and elutes were cleaned-up on Florisil® columns and screened for pesticides. For each compound, the method quantitation limit (MQL) was 1 ppb, and the method detection limit (MDL) was 0.33 ppb.

Gas chromatography with tandem mass spectrometry

Subsequent to analysis of ACMs collected in 1999, we learned GC with tandem mass spectrometry (GC-MS/MS) can be more sensitive for detecting certain contaminants than GC-ECD (Sheridan and Meola 1999). Therefore, ACMs collected in 2001 were analyzed with GC-MS/MS by the Agricultural Experiment Station Analytical Laboratory at Montana State University, Bozeman. Analyses followed procedures in Sheridan and Meola (1999). ACMs were screened for six of the 32 compounds screened in the 1999 panel including chlorpyrifos, endosulfan I, endosulfan II, endosulfan sulfate, *cis*-permethrin, and *trans*-permethrin (Table 1). ACMs were also screened for carbaryl, a chemical not included in the 1999 panel (Table 1) but listed for control of ACM larvae in ID, NE, and SD. The MQLs for GC/MS-MS analyses ranged from 10-60 ppb.

RESULTS

The GC-ECD analyses indicate ACMs contain pesticide residues only in trace amounts (Table 2). Across all sampling sites and per ACM, twelve chemical compounds were found in amounts \geq MQL. Of these twelve, seven were found in amounts of <1 ng ACM⁻¹. Five of the twelve were found in amounts ≥ 1 ng ACM⁻¹.

Permethrin was the chemical detected in the highest amount (10 ng ACM⁻¹) in ACMs collected in 1999 (Table 2). If each of the 40,000 ACMs a 115 kg bear could eat in a day contained 10 ng of permethrin, it could consume 0.003478 mg kg·bw⁻¹ per day (Table 3). Other chemicals found in ACMs at amounts ≥ 1 ng ACM⁻¹ were β -HCH, diazinon, and

heptachlor epoxide, which were found at levels of 1, 3, and 1 ng ACM⁻¹, respectively (Table 2, Table 3). The most liberal estimates of the amounts of these chemicals a bear could eat in a day are 0.000347, 0.001043, and 0.000347 mg kg·bw⁻¹ for β-HCH, diazinon, and heptachlor epoxide, respectively. None of these chemicals reached reported lethal or physiologically toxic levels in mammals (Table 3).

We did not observe temporal differences in pesticide levels in ACMs collected from Absaroka site 1 in 1999 (Table 2). ACMs from Absaroka site 2 contained almost twice as much permethrin as ACMs from other sites (Table 2). Pesticide levels detected in ACMs from New Mexico were similar to those of ACMs from Wyoming.

We did not detect chemicals in the ACMs collected in 2001 and screened by GC-MS/MS (Table 1).

DISCUSSION

Potential chemical toxicity to bears

Our results indicate that although pesticides are present in ACMs in trace quantities, they are likely insufficient to cause direct effects on or to biomagnify in bears.

Analyses of toxicant levels in grizzly bear lipids have not been performed to date, and therefore, we could not calculate biomagnification factors for the chemicals we detected. Hence, we evaluated potential threats of these chemicals to bears based on their levels in ACMs and by comparing these levels to published toxicity values for the most closely related species to bears for which data exist (Table 3). Bears may be more or less sensitive than

these species. To calculate conservative estimates of daily chemical ingestion by bears we used the maximum number of ACMs a bear can eat in a day and the maximum chemical levels detected in ACMs (Table 3). Thus, it is likely bears are not ingesting chemical levels approaching our estimates.

During this study, permethrin was listed for controlling ACM larvae in the states of NE and WY but not in the states of ID, MT, and SD. If bears are as sensitive to permethrin as are dogs (*Canis familiaris*), bears would have to eat >1,400 and >40,000 times their estimated maximum daily ingestion rate to experience chronically toxic and endocrine disrupting effects, respectively (Table 3). The World Health Organization (WHO) acceptable human daily dietary intake (ADI) and the U.S. Environmental Protection Agency (EPA) acceptable daily dose for humans over a 70-year lifetime (RfD) for permethrin are >14 times what a bear could potentially ingest in a day of eating ACMs (Lu 1995; Kamrin 1997) (Table 3). These estimates indicate bears are not consuming amounts that are likely to be physiologically toxic. Permethrin does not persist in environments or bioaccumulate (Smith and Stratton 1986) and is unlikely to biomagnify in bears.

Although diazinon was not listed for controlling ACM larvae in the states of ID, MT, NE, SD, and WY, in 1999 it was detected in ACMs at Absaroka site 1 in trace amounts (Table 2). If bears are as sensitive to diazinon as are swine (*Sus spp.*), they would have to consume >9,500 and >1,400 times their estimated maximum daily ingestion rate to experience chronically toxic or endocrine disrupting effects (Table 3). The WHO ADI for diazinon is 1.9 times the maximum daily amount we estimated bears could ingest. At this rate bears would be eating 1.2 times the EPA RfD (Table 3). Diazinon does not appear to

bioaccumulate, and bears do not consume physiologically toxic levels. However, our estimates indicate bears could potentially consume more than the acceptable daily level established by the EPA for humans.

ACMs could incorporate diazinon in various ways. Although it was not listed for controlling ACM larvae in ID, MT, NE, SD, WY, it has been recommended for controlling other pests that feed on crops also eaten by ACM larvae (e.g. sugar beets) (Hein 2003). So, it is possible that ACMs were not targets of diazinon control, but that they became contaminated with it. Alternatively, ACMs could have migrated to the mountains from states where use of diazinon was recommended. Also, diazinon is commonly found in air, rain, and fog (EPA 2001). Hence, it is possible ACMs became contaminated via these mediums.

β -HCH was not listed for controlling ACM larvae in ID, MT, NE, SD, and WY during this study, but it was detected in 1999 in trace amounts (Table 2, Table 3). If bears are as sensitive to β -HCH as are rats (*Rattus* spp.), they would have to consume >14,000 and >11 times the estimated maximum daily ingestion rate to reach chronically toxic and endocrine disrupting levels, respectively (Table 3). There is currently no WHO ADI or EPA RfD for β -HCH. Therefore, we cannot determine whether bear consumption could be higher than the amounts acceptable for humans.

Neither heptachlor nor chlordane was listed for controlling ACM larvae, yet their metabolite heptachlor epoxide was detected at low levels in 1999 (Table 2, Table 3). Bears would have to consume >280 and >1,400 times their estimated maximum daily ingestion rate to reach chronically toxic and endocrine disrupting levels (Table 3). This rate is >3.4 times the WHO ADI and >26 times the EPA RfD. Therefore, although bears ingest levels below

those causing physiological toxicity, they could potentially consume amounts greater than those considered acceptable for humans.

The parent compounds of β -HCH (e.g. technical HCH) and heptachlor epoxide (e.g. heptachlor, chlordane) were banned in the U.S.A. in the 1970s and 1980s (ATSDR 1993, ATSDR 2003). Lindane, also a parent compound of β -HCH, has been restricted to specific seed treatments (ATSDR 2003). Hence, detection of β -HCH and heptachlor epoxide in ACMs likely results from historic use of their parent compounds and their persistence in environments (Oliver and Nimi 1988; ATSDR 1993; Zhu and Norstrom 1993). Although bears are not consuming physiologically toxic amounts of β -HCH and heptachlor epoxide they may potentially bioaccumulate in bears over time. However, the potential of moths to transport these chemicals will decrease as residues of their parent compounds decrease in the environment over time.

Although we were unable to analyze ACMs for residues of all chemicals listed for controlling larvae, we did analyze ACMs for residues of pesticides commonly listed and representing each of the four chemical classes listed to control larvae. Additionally, that GC-MS/MS did not detect chemicals detected by GC-ECD is not surprising because the GC-MS/MS analysis was less sensitive (i.e. the MQLs were higher than those for GC-ECD).

MANAGEMENT CONSIDERATIONS

Results of this study indicate that ACMs do not transport biologically significant (i.e. physiologically toxic) levels of contaminants to high elevations and minimize concerns of

chemical bioaccumulation in bears under current pesticide use. The low to undetectable levels we report are logical because ACMs produce most of their fat body in the alpine where pesticides are not used.

However, pesticide use remains relevant to bear conservation. When compared to domestic species typically used to determine chemical toxicities, bears have unique physiology including hyperphagia, brown fat accumulation, and torpor. This could result in differences in their assimilation or excretion of certain chemicals, particularly those stored in fat. Also, because available pesticides and their listed uses change, we recommend repeating this work as necessary in the future. We also recommend collection and pesticide residue analysis of grizzly bear tissue. These analyses should be performed on grizzly bear fat, blood or hair samples (Tsatsakis and Tutudaki 2004 and references therein) taken from bears suspected of feeding at moth sites. Care must be taken to eliminate alternative sources of pesticides as they could confound residue levels attributable to ACMs. Additionally, we could not find literature documenting synergisms between the chemicals detected in ACMs. If synergisms are discovered, future studies will need to consider their effects.

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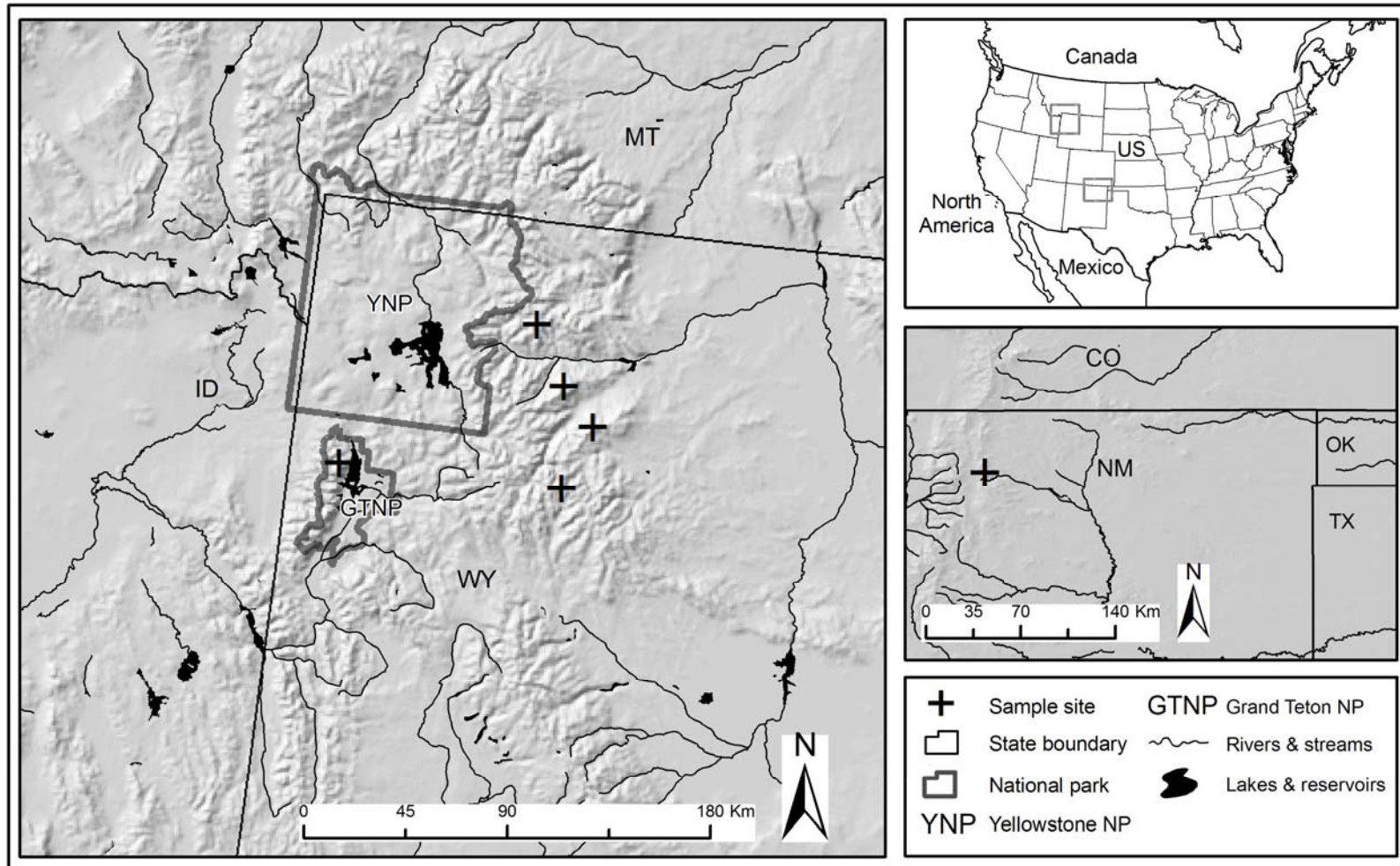


Figure. 1. ACM sampling sites in the Greater Yellowstone Ecosystem (N=5) and New Mexico (N=1), 1999-2001.

Table 1. Chemical compound screened, commercial name, chemical class, analysis method, and state where chemical was listed for controlling ACM larvae (USDA 2001; NDSU 2001a; NDSU 2001b).

Chemical compound	Commercial name ^a	Chemical class ^b	Analysis method ^{c,d}	State where listed for control ^e
Aldicarb	Temik	C	n.a.	MT,WY
α -BHC, β -BHC, δ -BHC	–	OC	GC-ECD	–
Bifenthrin	Capture	P	n.a.	MT
Carbaryl	Sevin	C	GC-MS/MS	ID,NE,SD
Carbofuran	Furadan	C	n.a.	WY
Chlorpyrifos	Lorsban	OP	GC-ECD, GC-MS/MS	ID,MT,NE,SD,WY
cis-Chlordane, trans-Chlordane	–	OC	GC-ECD	–
Cyfluthrin	Baythroid, Tempo	P	n.a.	NE,SD
Dacthal	–	Alkyl phthalate	GC-ECD	–
o,p'-DDD,	–	OC	GC-ECD	–
p,p'-DDD	–	OC	GC-ECD	–
o,p'-DDE,	–	OC	GC-ECD	–
p,p'-DDE	–	OC	GC-ECD	–
o,p'-DDT,	–	OC	GC-ECD	–
p,p'-DDT	–	OC	GC-ECD	–
Diazinon	–	OP	GC-ECD	–
Disulfoton	Di-Syston	OP	n.a.	WY
Dieldrin	–	OC	GC-ECD	–
Endosulfan, Endosulfan II, Endosulfan sulfate	Phaser, Thiodan	OC	GC-ECD, GC-MS/MS	MT
Endrin	–	OC	GC-ECD	–
Esfenvalerate	Asana XL	P	n.a.	MT,NE,SD
HCB,	–	OC	GC-ECD	–
Hexachlorobenzene	–	OC	GC-ECD	–
Heptachlor, Heptachlor epoxide	–	OC	GC-ECD	–
Lambda cyhalothrin	Warrior, Karate	P	n.a.	MT,NE,SD,WY
Lindane	–	OC	GC-ECD	–
Malathion	Malathion	OP	n.a.	WY
Methomyl	Lannate	C	n.a.	ID,MT,NE
Methoxychlor	Marlate	OC	GC-ECD	MT
Methyl parathion	Methyl Parathion, Pennacap-M	OP	n.a.	ID,NE,WY
Mirex	–	OC	GC-ECD	–
cis-Nonachlor,	–	OC	GC-ECD	–

trans-Nonachlor				
Oxychlorthane	–	OC	GC-ECD	–
PCA, Pyrazon	–	Pyridazinone	GC-ECD	–
cis-Permethrin, trans-Permethrin	Pounce, Ambush	P	GC-ECD, GC- MS/MS	NE, WY
Terbufos	Counter	OP	n.a.	MT, WY
Trifluralin	–	2,6- dinitroaniline	GC-ECD	–

^a common names of some commercial products containing compound in first column.

^b C, carbamate; OC, organochlorine; OP, organophosphate; P, pyrethroid.

^c GC-ECD, gas chromatography with electron capture detection; GC-MS/MS, gas chromatography with tandem mass spectrometry.

^d n.a. indicates chemicals for which ACMs were not screened.

^e – indicates chemicals not listed for control at the time of this study or those that were no longer registered for use.

Table 2. Aggregation sites where ACMs were collected organized by date, elevation, number of moths in sample (n), and chemical compound levels in the samples in ng ACM⁻¹ when analyzed by GC-ECD^a.

Aggregation site	Date	Elevation	n	Compound	ng ACM ⁻¹
Absaroka site 1	13 July 1999	3400 m	60	o,p'-DDD	<1
				Diazinon	1
				Heptachlor	<1
				Heptachlor Epoxide	<1
				Oxychlorane	<1
				cis-Permethrin	4
				trans-Permethrin	3
Absaroka site 1	2 Aug. 1999	3400 m	49	o,p'-DDD	<1
				Heptachlor	<1
				Heptachlor Epoxide	<1
				cis-Permethrin	2
Absaroka site 1	3 Aug. 1999	3400 m	50	trans-Permethrin	2
				Chlorpyrifos	<1
				o,p'-DDD	<1
				Oxychlorane	<1
Absaroka site 1	19 Aug. 1999	3400 m	69	cis-Permethrin	4
				trans-Permethrin	3
				β-BHC	<1
				Dacthal	<1
Absaroka site 2	21 July 1999	3438 m	50	Oxychlorane	<1
				cis-Permethrin	5
				trans-Permethrin	4
				β-BHC	1
Absaroka site 3	26 July 1999	3390 m	52	Diazinon	3
				Heptachlor	<1
				Heptachlor Epoxide	1
				cis-Permethrin	10
Absaroka site 4	15 Aug. 1999	3352 m	78	trans-Permethrin	10
				Heptachlor Epoxide	<1
Absaroka site 4	15 Aug. 1999	3352 m	78	Oxychlorane	<1
				Diazinon	<1
				Heptachlor Epoxide	<1
				Mirex	<1
New Mexico site	23 Aug. 1999	3645 m	28	Oxychlorane	<1
				cis-Permethrin	6
				trans-Permethrin	4
				β-BHC	<1
Teton site	25 Aug. 1999	3075 m	38	p,p'-DDE	<1
				Diazinon	<1
				Heptachlor Epoxide	<1
				Oxychlorane	<1
Teton site	25 Aug. 1999	3075 m	38	cis-Permethrin	4
				trans-Permethrin	4
				Oxychlorane	<1
Teton site	25 Aug. 1999	3075 m	38	cis-Permethrin	5
				trans-Permethrin	4

^a other compounds not listed were <MQL of 1 ppb and <MDL of 0.33 pp.

Table 3. Chemicals detected in ACMs >MQL, highest amounts, amount a bear could potentially eat in a day based on consuming 40,000 ACMs, LD₅₀s, amount a bear would have to eat to experience carcinogenic (C), chronic (CH), endocrine disrupting (ED), reproductive (R), or teratogenic (T) effects, the WHO ADI, and the U.S. EPA RfD.

Chemical	Highest chemical amount found in ACMs	Chemical amount a bear could eat in a day	LD ₅₀	mg kg ⁻¹ per day a bear would have to consume to incur physiologically toxic effects					WHO ADI	EPA RfD
	ng ACM ⁻¹	mg kg ⁻¹	mg kg ⁻¹	C	CH	ED	R	T	mg kg ⁻¹	mg kg ⁻¹
β-BHC	1	0.000347	2000 ^{a,f}	≥0.37 ^{b,g}	≥0.5 ^{a,f}	≥0.004 ^{b,h}	≥0.5 ^{a,f}	no≤0.1 ^{a,f}	n.a. ⁱ	n.a. ^j
Diazinon	3	0.001043	143 ^{e,k}	no≤45 ^{a,l}	≥10 ^{c,l}	≥1.5 ^{a,m}	≥1.5 ^{a,m}	≥1.0 ^{d,l}	0.002 ⁱ	0.0002 ⁿ
Heptachlor epoxide	1	0.000347	39 ^{a,o}	≥1.2 ^{a,l}	no≤0.1 ^{d,l}	≥5 ^{a,p}	≥0.5 ^{a,q}	≥5 ^{a,l}	0.0005 ^r	1.3x10 ^{-5j}
Permethrin	10	0.003478	430 ^{a,l}	no ^{a,s}	no≤5 ^{d,l}	no≤150 ^{a,t}	≥250 ^{a,l}	no≤1800 ^{a,s}	0.05 ^l	0.05 ^l
Chlor-pyrifos	<1	<0.000347	=82 ^{a,k}	no≤10 ^{a,l}	≥1 ^{d,l}	Yes ^u	no≤1 ^{a,l}	≥15 ^{a,l}	0.01 ^l	0.003 ^l
Dacthal	<1	<0.000347	≥3,000 ^{a,l}	no≤500 ^{a,l}	≥800 ^{d,l}	Yes ^v	no≤500 ^{a,l}	no≤300 ^{e,l}	n.a. ^l	0.01 ^w
Heptachlor	<1	<0.000347	=40 ^{a,k}	≥1.2 ^{a,l}	no≤0.1 ^{d,l}	Yes ^x	≥0.25 ^{a,l}	≥5 ^{a,l}	0.0001 ^l	0.005 ^l
Mirex	<1	<0.000347	=100 ^{d,k}	≥0.25 ^{a,y}	≥0.25 ^{a,y}	Yes ^x	≥0.25 ^{a,y}	≥6 ^{a,y}	n.a. ^y	0.0002 ^z
Oxy-chlordane	<1	<0.000347	=19.1 ^{a,a1}	no≤2 ^{a,a1}	≤2 ^{a,a1}	≥0.1 ^{a2}	no≤1.5 ^{a,a1}	≥3 ^{a,a1}	≤0.001 ^{a1}	0.0005 ^{a3}
o,p'-DDD	<1	<0.000347	>4000 ^{a,a4}	no<0.3 ^{a,a4}	no<0.3 ^{a,a4}	Yes ^{x,a5}	no<0.3 ^{a,a4}	Yes ^{a6}	0.005 ^{a7}	0.0005 ^{a8}
p,p'-DDE	<1	<0.000347	>880 ^{a,a4}	>7.21 ^{b,g}	no<0.3 ^{a,a4}	≥200 ^{a,a9}	no<0.3 ^{a,a4}	Yes ^{a6}	0.005 ^{a7}	0.0005 ^{a8}

^a rat, ^b human, ^c swine, ^d dog, ^e rabbit, ^f WHO 1991, ^g Quintana et al. 2004, ^h Akkina et al. 2004, ⁱ Lu 1995, ^j EPA IRIS 2002, ^k Ramamoorthy et al. 1995, ^l Kamrin 1997 and references therein, ^m El Aziz et al. 1994, ⁿ EPA 2004a, ^o ATSDR 1993, ^p Wango et al. 1997, ^q WHO 1975, ^r WHO 1984b, ^s WHO 1990, ^t Kunimatsu et al. 2002, ^u Andersen et al. 2002, ^v Colborn and Short 1999, ^w EPA 2004b, ^x Colborn et al. 1993 (and sources therein), ^y WHO 1984c, ^z EPA 2004c, ^{a1} WHO 1984a, ^{a2} Cassidy et al. 1994, ^{a3} EPA 1997-value for parent compound chlordane, ^{a4} WHO 1979, ^{a5} Klotz et al. 1996, ^{a6} Dorner and Plagemann et al. 2002-parent compound DDT, ^{a7} WHO 1979-value for parent compound DDT, ^{a8} EPA 2004d-value for parent compound DDT, ^{a9} Kelce et al. 1997. no = no reported effect in these sources at or below levels indicated at the time of this writing. n.a. = no level available at this time.

CHAPTER 4

The spatial probability of an interspecific relationship – describing and predicting habitat used by army cutworm moths and grizzly bears in the Greater Yellowstone Ecosystem

INTRODUCTION

Army cutworm moths (*Euxoa auxiliaris*) migrate from low elevations in the Great Plains and Intermountain West to high elevations in the Rocky Mountains and aggregate in alpine talus from July through September before returning to low elevations in the fall (Pruess 1967). Grizzly bears (*Ursus arctos horribilis*) consume the moths by the millions over the summer. When compared with other foods, moths, at 8 kcal/g, are the richest food available to grizzly bears in the Greater Yellowstone Ecosystem (GYE) (French *et al.* 1994). By late summer, lipids comprise 70-83% of the moths' body mass (Kevan and Kendall 1997, White *et al.* 1999), and in 30 days of feeding extensively on moths a bear can consume close to half of its yearly energy needs (Sizemore 1980, White 1996).

Grizzly bears in the lower 48 states of the U.S.A. were listed as threatened under the U.S. Endangered Species Act in 1975 (USFWS 1993). Due to conservation efforts, the bear population in the Greater Yellowstone Ecosystem (GYE) (Figure 1, Chapter 1) was delisted in 2007 (USFWS 2007). In September 2009, a judge in Montana ruled in favor of re-listing the bear, and federal protections have been reinstated (USFWS 2009). Prior to this the USFWS' *Conservation Strategy* was the guiding document for the bear's

conservation since its delisting (USFWS 2007a, 2007b). The *Strategy* described roles for managing bears for the Fish and Game Departments of Idaho, Montana, and Wyoming and the Federal Government. The *Strategy* allowed bears to expand into biologically suitable and socially acceptable areas within and beyond the prescribed Primary Conservation Area (PCA) (Figure 1, Chapter 1). The *Strategy* also mandated the use of georeferenced habitat data to aid in monitoring the four major grizzly bear foods (moths, cutthroat trout [*Oncorhynchus clarki*], whitebark pine [*Pinus albicaulis*] seeds, and winter-killed ungulates [*Bison bison*, *Cervus elaphus*, *Alces alces*, *Odocoileus hemionus*]) and to identify habitats into which bears may expand (USFWS 2007b). The 2009 ruling nullified the *Strategy*; however, monitoring critical bear foods and identifying potentially suitable habitat for bears will remain essential to any plan to manage bears in the GYE. Any plan that may replace the *Strategy* also will require agencies to focus their limited resources to monitor the four major foods, design flight plans with which to estimate population size, plan access management to sensitive areas used by bears, strategize adaptive management programs, provide people with education on how to live and recreate safely with bears, secure funding for bear conservation projects, and facilitate understanding of and support for grizzly bear recovery.

In order to monitor the four critical bear foods, biologists and managers need to know where these foods occur or might occur. Biologists and managers in the GYE know where cutthroat trout, whitebark pine seeds, and winter-killed ungulates tend to occur in the GYE, and there are currently survey methods with which to determine their availability to bears.

Biologists found the moth sites used by bears in the GYE by observing bears using talus slopes during observation flights, ground checking the sites, and discovering evidence of bears feeding on moths (Mattson *et al.* 1991). In areas beyond the PCA where grizzly bears do not currently live, biologists cannot rely on sightings to indicate where moths occur. Moth aggregation sites are widely scattered in remote wilderness areas, and trying to identify moth sites on the ground is time intensive, physically demanding, and expensive. Therefore, it is inefficient to spend human and financial resources to look for moth aggregation sites without having a tool (*i.e.*, a model) with which to narrow the search area.

Models of resource selection by species range from general to specific. For example, general models may define or predict species distribution or occurrence, and specific models may generate measures of habitat use. Both general and specific models vary in scale due to the biology of a species or the goal of a study. Explanatory models attempt to provide insight into ecological processes that produce patterns (*e.g.*, species presence) with respect to environmental variables such as solar radiation, habitat type, etc. by examining their relationships statistically (Guisan *et al.* 2002). Predictive models seek both to describe a statistical relationship between the response and environmental variables and to use this relationship to predict species occurrence or estimate species numbers in new, unsampled locations (Guisan *et al.* 2002). Geographic information systems (GIS) and georeferenced spatial data (*e.g.*, vegetation, hydrology, geology) work in concert with statistical models and are analyzed and evaluated using a variety of methods (Guisan *et al.* 2002, Boyce *et al.* 2002, Hirzel *et al.* 2006, Thomas and Taylor 2006). Models of resource selection exist for many taxa such as tigers (*Panthera tigris*),

Smith *et al.* (1998); lynx (*Lynx lynx*), Zimmermann and Breitenmoser (2002); grizzly bears (*Ursus arctos*), Nielsen *et al.* (2002); wolverines (*Gulo gulo*), Krebs *et al.* (2007); terrestrial invertebrates, Fleishman *et al.* (2001); aquatic invertebrates, Manel *et al.* (2000); various birds, Saveraid *et al.* (2001); grouse (*Tympanuchus phasianellus*), Goddard *et al.* (2009); and alpine plants, Guisan *et al.* (1998).

Models include resource selection functions (RSF) and resource selection probability functions (RSPF); the main difference between these is that RSPFs estimate probability of use whereas RSFs only rank resource units with respect to use (Thomas and Taylor 2006). The goals of these studies vary and include examining opportunities for connectivity in fragmented landscapes (*e.g.*, Smith *et al.* 1998, Pudu *et al.* 2009), predicting habitat correlates of where species may occur in the environment (*e.g.*, Fleishman *et al.* 2001, Saveraid *et al.* 2001), and estimating species richness (Owen 1989) or biodiversity (Ko *et al.* 2009). A rich literature exists on both the various types of data, designs, and evaluation techniques for different research goals (Thomas and Taylor 1990, Fielding and Bell 1997, Guisan and Zimmerman 2000, Austin 2002, Boyce *et al.* 2002, Guisan *et al.* 2002, Scott *et al.* 2002, Pearce and Boyce 2005, Thomas and Taylor 2006, Hirzel *et al.* 2006) and the interpretation and application of various analyses (Cherry 1996, Fielding and Bell 1997, Boyce *et al.* 2002, Keating and Cherry 2004, Strickland and McDonald 2006, Thomas and Taylor 2006).

My goal in this chapter is to model the spatial probability of the interaction between grizzly bears and moths in the GYE and, in doing so, create a tool with which biologists can identify habitat that bears and moths may use within the PCA and that bears may expand into beyond the PCA in search of moths. I developed models using the

characteristics of sites where bears forage for moths and random sites I selected throughout the area in which bears are known to feed on moths. Because moths may seek certain areas within the talus (French *et al.* 1994, White *et al.* 1998b) and because different geologies have different thermal and fracturing properties, I hypothesized that surficial geology (*e.g.*, surface layers, such as soil, exposed bedrock, or glacial deposits) would be a significant predictor describing these areas. Based on descriptions of these sites in the literature (Mattson *et al.* 1991, French *et al.* 1994, O'Brien and Lindzey 1994, White *et al.* 1998a) and personal observations, I expected elevation, topographic roughness, and slope each would be significant predictors of these sites. Because sites often are found below headwalls, cirques, arêtes, and cols (Mattson *et al.* 1991, French *et al.* 1994) I investigated whether geomorphic features such as contours (*e.g.*, gullies, ridges) and the rate of change in slope might describe sites. Studies suggest sites are found on certain aspects (Mattson *et al.* 1991, O'Brien and Lindzey 1994, White *et al.* 1998a), but they did not test the significance of aspect, so I investigated the significance of aspect as a descriptor of these sites. A measure of heat loading of slopes may help describe sites used by moths and bears because heat loading will influence snow melt, plant species and flowering times, and the temperature gradient within the talus. Landsat Thematic Mapper (TM) imagery and transformations of it are useful in discriminating geological features (Perez *et al.* 2006). Additionally, bear habitat use has been found to correspond with transformed Landsat TM spectra (Nielsen *et al.* 2002). For these reasons, I investigated the whether there was a significant relationship between transformed Landsat TM data and areas used by moths and bears.

STUDY AREA

The study area, the GYE, is in northwestern Wyoming and adjacent lands in Idaho and Montana (Figure 1, Chapter 1). The GYE includes Yellowstone and Grand Teton National Parks, six adjacent national forests, and state and private lands in Idaho, Montana, and Wyoming. The GYE comprises the Yellowstone Plateau and 14 surrounding mountain ranges above 1,500 m (Anderson 1991, Patten 1991, Schwartz *et al.* 2006), which reach elevations of ~4,200 m at their highest points, Gannett Peak in the Wind River Range and Grand Teton Peak in the Teton Range. Deep valleys, cirques, sharp ridges, and floodplains characterize the mountain ranges within the GYE (Smith *et al.* 1993, Sundell 1993, Love *et al.* 2003). Climate, geology, hydrology, precipitation, vegetation, and fauna have been described previously (Waddington and Wright 1974, Despain 1990, Marston and Anderson 1991, Clark *et al.* 1999). Army cutworm moths aggregate in talus at elevations between 2,768 – 3,680 m near the base of large headwalls above timberline (Mattson *et al.* 1991, French *et al.* 1994, O'Brien and Lindzey 1994). The talus in which moths aggregate typically contains rocks measuring 8-40 cm and lacks vegetation (Mattson *et al.* 1991). The alpine tundra and meadows adjacent to these sites support the flowering plants on which the moths feed.

METHODS

The data

The data I used to develop models were environmental variables extracted from both “used” and “available” sites. I obtained and analyzed independent samples of used and available units (Thomas and Taylor 2006). Based on a conservative rule for sample size

determination for binomial distributions as discussed by Adcock (1997) and Thompson (1987), I chose a sample size of $n \geq 400$ for an error rate (d) of 0.05 in which $n \geq 0.25\chi^2_{(1),\alpha}/d^2$.

The dataset included 301 unduplicated sites both where bears were observed feeding in talus from 1982 through 2002 and where moths were known to occur. I considered these sites “used” and assigned them a value of 1. To characterize a sample of available habitat, I generated a random sample of 1000 points in ArcGIS (ESRI Inc. © 1999-2006, Hawth’s Analysis Tools version 3.27© 2002-2006) within a polygon that encompassed all locations used by bears foraging on moths. I considered these sites “available” and assigned them a value of 0. Hence, the sampling unit was a used or available location. I included locations bears used multiple times only once in the dataset, and locations were included either in the “used” sample or in the “available” sample, but not in both (Thomas and Taylor 2006). I restricted my selection of random points to a lower bound of 3009 m in elevation, because that was the lowest elevation at which bears were observed to forage in this dataset and in the literature bears feed on moths at this elevation approximately or above it (Mattson *et al.* 1991, French *et al.* 1994). Including areas below 3009 m would have included locations that might not actually be “available” to bears and moths. Points were buffered by 30 m to incorporate error associated with locations made by aerial observations. Additionally, the digital elevation model (DEM) for the GYE and Landsat Thematic Mapper (TM) 7 imagery had a resolution of 30m.

Based on relationships reported in studies of bears foraging on moths and on personal observations, I selected a suite of environment variables I reasoned might be significant descriptors of sites. I extracted the variables from buffered used and available points

(Table 1). I considered 17 continuous and 1 categorical environmental variables. For continuous variables I also considered their standard deviations to incorporate the variability of these variables within the buffered points. I calculated from a 30 m DEM elevation, an index of heat-loading of terrain (Parks 2004), aspect linearized into EW and NS components, an index of topographic roughness (Evans 2004), slope, profile (*i.e.*, the rate of change in slope), and planimetry (*e.g.*, gullies, ridges) (Table 1).

Tasseled cap (Crist *et al.* 1986) and principal components transformations remove correlations that exist among raw data from the six Landsat TM bands and generate new bands. I therefore performed tasseled cap and principal components transformations in ENVI (version 4.3, ITT Visual Information Solutions © 2008) and ArcGIS, respectively. Tasseled cap transformation produces three bands, brightness, greenness, and wetness (Table 1). Principal components transformation generates the same number of bands, in this case six, as are entered into the transformation (Table 1). I extracted surficial geology from a digital layer for the study area (Case *et al.* 1998) using Hawth's Tools (Hawth's Analysis Tools version 3.27© 2002-2006) (Table 1). The variable surficial geology comprises seven levels, including glaciated areas, glacial deposits, landslides, bedrock, residuum, slopewash, and colluvium. Colluvium (*i.e.*, loose rock that collects at the base of slopes) was the reference category in statistical analyses. Since I buffered used and available points, I extracted the average value from each buffered point (*i.e.*, polygon); in the case of surficial geology, which is a categorical variable, I extracted its value from the center of each polygon (Table 1).

Exploratory data analysis

I reviewed summary statistics for these data, inspected univariate histograms and Q-Q normal plots for each variable to determine whether these data required transformations to meet model assumptions, and viewed bivariate graphs of variables (*i.e.*, matrix scatterplot, correlation matrix) to check for patterns and correlations among variables. I also used boxplots to assess the degree of association between each environmental variable and the response variable (*i.e.*, used-available). I plotted the relationship between each environmental variable and the response variable using a generalized additive model (gam) function in S-plus to investigate whether each relationship approached a logistic function.

Modeling procedure

This was a design 1-type study (Thomas and Taylor 2006) where data are at the population level, and individual animals, although recorded, are not the unit of analysis (Manly *et al.* 2002, Thomas and Taylor 2006). In this study, the unit of analysis was the location, and the goal was to fit a logistic regression model for a sample of locations (*i.e.*, plots) (Thomas and Taylor 2006). The data type employed was use-availability.

I used generalized linear model (GLM) with a binomial distribution and a logit-link function in S-plus 8.1 (TIBCO Spotfire S+® 8.1 for Windows © 2008). I used correlations and box plots between environmental variables and the response to help determine which environmental variables to use in modeling. For example, if a environmental variable correlated with both the response and another environmental variable ($r > 0.4$), I chose the environmental variable with both a box plot that indicated it

might be informative (*i.e.*, the means were different between used and available states and overlap of interquartiles was minimal) and a higher correlation with the response over the competing environmental variable. I started with models based on combinations of variables that were not correlated with each other and refined them following stepwise procedures based on Akaike's Information Criterion (AIC) (Akaike 1973) and reductions in deviance as measured by the χ^2 statistic (Guisan *et al.* 2002). I chose the best model as the one with the lowest AIC score and the least residual deviance after fitting the model. Where differences between model AIC scores were less than 2, I considered the models identical (Burnham and Anderson 2002).

I evaluated each of the best models using both threshold dependent (Kappa) and independent (K_{\max} , ROC) measures. Using classification matrices I generated from model predictions, I assessed true positives and true negatives as well as two types of error, false positives, and false negatives (Fielding and Bell 1997). The cut-off threshold selected for assigning a predicted value a 1 (*i.e.*, used) or a 0 (*i.e.*, unused or available) in a model confusion matrix influences some measures (Fielding and Bell 1997). Therefore, I calculated model sensitivity (the proportion of true positives correctly classified), specificity (the proportion of true negatives correctly classified), and overall classification accuracy (the proportion of sites correctly classified) from confusion matrices for each model over a spectrum of thresholds (Fielding and Bell 1997). Kappa (K) (Cohen 1960) is an index of the agreement between model prediction and the data, where 0 corresponds to random agreement; it also is calculated from the confusion matrix and is threshold dependent. Therefore, I calculated K_{\max} (Guisan *et al.* 1998), which is threshold independent; it is the highest Kappa attained when varying the threshold from 0

to 1 (Hirzel *et al.* 2006). Additionally, I constructed receiver operating characteristic (ROC) curves, which are threshold independent (Fielding and Bell 1997). I calculated D^2 , which is the proportion of the deviance in the data set accounted for by the model where a perfect model has no residual deviance and its D^2 is 1. I calculated D^2_{adj} (Guisan and Zimmerman 2000), which adjusts D^2 to account for the number of observations (n) and the number of predictors (p) in the model. I compared D^2_{adj} among models that included different combinations of variables. I considered the model with the lowest AIC score to be better than alternative models. I conducted five-fold crossvalidation for the top models by randomly dividing the data into five equal-sized subsets estimating model coefficients using four subsets and classifying the remaining subset (Fielding and Bell 1997, Boyce *et al.* 2002). I also used crossvalidation to resample the data and estimate both the number of misclassifications and the misclassification rate for each model at different cut-off thresholds. I performed all data analyses in S+® 8.1 (TIBCO Spotfire S+® 8.1 for Windows © 2008). Finally, I generated maps of the best models in ArcGIS using the Raster Calculator function in ArcTool Box (ESRI Inc. © 1999-2006).

RESULTS

Exploratory data analysis

The distributions of environmental variables (*i.e.*, histograms, Q-Q normal plots) indicated some departure from normality for variable heat-load. The distributions of other variables approximated a normal distribution, and transformations did not improve the distributions of these variables noticeably. I transformed heat-load using the log base 10 to normalize its distribution.

Correlation matrices and correlation coefficients indicated potential problems with multicollinearity among roughness, slope, and elevation-sd ($r \geq 0.85$) and between the principal component 2 and both wetness ($r = 0.96$) and brightness ($r = 0.91$), principal component 1 with brightness ($r = 0.99$) and wetness ($r = 0.67$). Additionally, box plots indicated that profile, planimetry, profile-sd, planimetry-sd, roughness-sd, dem-sd, brightness, and principal component 1 were not informative variables.

Modeling procedure, fitting and selection

I chose and tested models that included different combinations of variables (Table 2). Wetness and principal component 2 were highly correlated, but they each were correlated with the response variable, and box plots indicated that they each might be informative. Roughness and slope both seemed to be informative, and they also were highly correlated. I fit models that included wetness or principal component 2 and roughness or slope. Variables that were included in different combinations in the models included elevation, heat-load (transformed by \log_{10}), roughness, slope, wetness, greenness, EW aspect, principal component 2, and surficial geology (Table 2). I dropped variables from the models based on AIC scores and χ^2 drop-in-deviance tests to yield final models (Table 3).

In general, surficial geology accounted for the largest drops in deviance in all models. In models 2, 3 and 4 the next greatest drops in deviance were contributed by transformed Landsat TM band values (either wetness or principal component 2) and elevation. In model 1, however, elevation followed surficial geology as the largest contributor to deviance reduction followed by wetness.

Aspect, heat load, and slope or topographic ruggedness were significant at $\alpha = 0.05$ in the models in which they occurred and contributed to AIC values (except for slope in model 4), but they did not account for much drop in deviance. In all models, predicted presences were positively associated with glacial outwash and negatively associated with glacial deposits, landslides, bedrock, residuum, and slopewash with respect to the reference category colluvium.

Model evaluation

Model 4 was best model based on its AIC score, D^2_{adj} , and K_{max} (Table 4, Table 5). The next best models, 2 and 3, were > 4 AIC points higher than model 4 but within 1 AIC point of each other indicating that they had similar support with respect to each other. Model 1 was 31 AIC points higher than model 4. Graphs of sensitivity, specificity, and classification accuracy at cut-off thresholds (*i.e.*, the threshold at which a predicted presence is classified as a presence) ranging from 0.2 to 0.7 showed that for models 2-4, sensitivity, specificity, and classification accuracy converged near a threshold of 0.23 (Figures 1-3). K_{max} was 0.50 for models for 2-4 indicating moderate agreement between model prediction and the data (Landis and Koch 1977, Fielding and Bell 1997, Guisan and Zimmerman 2000). I generated a ROC curve for models 2-3 and plotted them together to evaluate them with respect to each other (Figure 4). The ROC curves arc well above the 45° line of random model performance (Figure 4). The ROC curve for model 3 indicated it performed a bit better at lower ranges and model 4 performed a bit better at higher ranges of 1 – specificity. Five-fold crossvalidation showed that model 4 generated

the lowest number of misclassifications (226) and had lowest misclassification rate (0.17).

I generated maps in ArcGIS for model 4 to describe spatially the statistical relationship between the environmental variables and the response (predicted ranks of bear and moth presence) where the response was binned into 10 levels ranging from low- (0) to higher- (1) rank (Figures 5-7). Because some predicted areas are small with respect to the study area, it is hard to observe all the predictions for all models in one large-scale view. Therefore, Figs. 5-7 show a subsample of mapped predictions in the Absaroka, Teton, and Wind River mountain ranges. In these figures I provide a larger-scale view on the left-hand side and break-out maps on the right-hand side that show a few selected areas in more detail. I inspected the maps visually to estimate both how well the model predicted the general area of sites used by bears and moths (green points in Figures 5-7). I also inspected how the model predicted sites ($n = 34$) previously inspected for moth presence (purple and blue points in Figures 5-7) (H. Robison, unpub. data).

DISCUSSION

My goal in this chapter was to model the spatial probability of the interaction between grizzly bears and moths in the GYE and, in doing so, create a tool to identify habitat that moths and bears may use within the PCA and that bears may expand into beyond the PCA in search of moths. Model 4 best describes the spatial probability of the interaction between moths and grizzly bears and the habitat used by moths and bears. It describes areas we know moths and bears currently use within the PCA, such as sites in the Absaroka Mountains, and it also predicts areas near those areas that bears are not

currently using. The model also predicts areas where interactions between these species may occur outside the PCA in the Wind River and Teton Mountain Ranges into which bears are expanding.

While logistic regression can be used to generate an RSPF to estimate the probability of use with random sampling of use-nonuse data, logistic regression analysis of use-availability data cannot be interpreted in the same way (Keating and Cherry 2004, Thomas and Taylor 2006). In models based on use-available data, such as the models in this study generated from independent samples of used and available units, the sample of available locations contains both used and unused sites (*i.e.*, used sites contaminate available sites at some unknown rate) (Keating and Cherry 2004). However, when the unconditional probability of use (q) is small, logistic regression provides an approximation for relative probability of use for use-available data in the form of relative ranks. The measure q equals N_1/N , where N_1 is the number of locations that are used (observed or not) by an animal and N is the number of locations available to an animal (Keating and Cherry 2004, Thomas and Taylor 2006). In this study I estimated that q was small (Keating and Cherry 2004). Therefore, I predicted relative ranks of use by moths and bears with logistic regression and mapped these in geographic space.

Evaluation of models requires consideration of a variety of factors. The choice of cut-off threshold for model predictions influences the classification matrix and the measures calculated from them including model sensitivity, specificity, classification accuracy, and K . With that in mind, in this study I used threshold dependent and independent measures to evaluate models. However, depending on the goal of a study, researchers can adjust thresholds to decrease the false negative rate at the expense of an

increased false positive rate (Fielding and Bell 1997). For example, a researcher can choose a threshold that yields more false positives (*e.g.*, a more “liberal” model for an endangered species) or fewer false positives if there is a greater need to find a true “hit” (*e.g.*, they need to focus their search due to resource or logistical constraints). That being said, these measures already may be biased low because of contamination in use-available data. Boyce and colleagues (2002) discuss that this may lead researchers to think their model is poor, when in fact it may not be. Even ‘perfect’ RSFs might not predict a value greater than some low value (Boyce *et al.* 2002).

The best model and the other models I report here indicate that surficial geology, elevation, and Landsat band values (wetness or principal component 2) are significant descriptors of these sites and that these variables cause relatively larger drops in deviance in models. Also, ruggedness, slope, aspect, and heat-load each were significant in the models in which they occurred and contributed to AIC values in most models; however, they did not contribute much to drops in deviance. These results support the hypotheses that surficial geology, elevation, and Landsat TM bands are important predictors of these sites but do not support the importance of topographic roughness, aspect, or slope. In these data wetness, brightness, and principal component 2 were highly correlated with each other. Together, as their pixel values increase, brightness and wetness provide information on soils. Specifically, brightness provides information on the texture, brightness, and moisture of soils with wetness adding additional information on these factors (Crist 1986). Glacial outwash, which may comprise talus, was positively associated with predicted presences with respect to the reference category colluvium.

Although K_{\max} indicated moderate agreement between the data and the best model's predictions, the explained deviance (D^2_{adj}) and model sensitivity are a bit low. However, I visually inspected the maps of model predictions with respect to sites that were visited and inspected for the presence of moths, and this revealed that the model performs fairly well qualitatively to indicate the general area in which moth sites occur (Figure 7). For example, although the model may not pick out the same pixel in which a bear and moth location occurred, it predicted areas near this pixel.

Inclusion of variables that associate with moth and bear use but were not used or available for modeling may improve model fit. For example, I did not include spatial autocorrelation in these models. Most ecological associations are not random but occur in spatially correlated patches (Legendre 1993). Therefore, I might expect that areas models predict moths and bears use are near those known to be used by moths and bears. Investigating the potential effects of spatial autocorrelation of features that associate with moth and bear use may help improve qualitative and quantitative model fit. Ground-truthing the model with existing data and collecting new data may assist this. Not including spatial autocorrelation usually inflates Type I error rates (*i.e.*, false positives) (Thomas and Taylor 2006). If this is true for my models, they would tend toward false positives. However, because a goal of this study was to create a tool to identify moth habitats, the cost of false positives in terms of resources and logistics may be lower than the cost of false negatives.

Another environmental factor that may influence moth and bear use is the presence of snowfields and/or streams because these features may influence the temperature gradient that moths seek (White *et al.* 1998b). French *et al.* (1994) and H. Robison (pers. observ.)

observed moths moving within talus over the summer, seemingly tracking snow and/or meltwaters in talus fields. It is possible that the wetness and principal component 2 were, in part, capturing brightness values associated with snow and/or ice near these sites. Water and/or ice and snow, may have been proxied by wetness and principal component 2, but it could be helpful to include data clearly attributing the former components. Additionally, major drainage basins that orient E-W may act to funnel migrating moths toward certain sites. Another variable that is hard to assess other than from the ground is the character of the interstitial space of the talus. Stereophotos and overflights might suggest that a site is suitable for bears and moths, but if the interstitial space of the talus is filled in then it will not provide the right environment for moths. For example, landslides that were negatively associated with predicted presence in this dataset may be associated with unfavorable interstitial space among rocks. Additionally, there may be a behavioral component contributing to moth site selection and aggregation of moths in talus. Moths begin mating in high elevations (H. Robison, Chapter 1), and they call to each other by releasing a pheromone. Conspecific effects such as this may influence habitat selection, but as of yet, they are rarely included in habitat models (Campomizzi *et al.* 2008). Additionally, bears search the talus with their noses close to the ground, and it is possible that the bears find the moths by smelling their pheromone. Restricting the sites I chose as available to sites within talus also might help improve model fit, but as of yet there is no georeferenced layer that describes talus within the study area. The moths feed throughout the summer, and availability of nectar sources is important (Kevan and Kendall 1997). However, the relationship between the distance of these resources and

talus sites used by moths has not been described quantitatively. There may be a distance at which moths do not travel from their talus refugia to forage.

In general, the ecological relationship between moths and bears is influenced by a number of factors including weather patterns that influence moth numbers in low elevations, the abundance of moths migrating to high elevations, the flower resources available to moths, the availability of talus and its thermal and structural characteristics, the security of moth sites from disturbance, and potentially the availability of other foods to bears during the time moths are available. With respect to high elevation habitat, specifically, one might expect that climate change will influence the community of flowers available to moths at high elevations. Moths, however, do not appear to be specialists (H. Robison, unpub. data), and the moths may be able to use other flowers as they expand upslope and replace existing plants. Temperature and aridity are thought to drive migration within the genus *Euoxa* (Pruess 1967, Hardwick and Lefkovitch 1971, Oku 1983). Therefore, the factors most likely to limit suitability of moth habitat are the temperature gradient within the talus provided by snow, ice, and their meltwaters and perhaps available water for nectar plants. The model presented here could be used to examine these possibilities if predicted sites become used by moths and bears.

Additionally, if currently used sites become unused by moths and bears, the model may provide a spatial reference for variables which that contribute to abandonment of sites.

Moth abundance is dynamic in time – it grows over the summer, peaks, and declines (White *et al.* 1998b). In some years fewer known moth aggregation sites are used than in other years (Bjornlie and Haroldson 2008). From this it has been inferred that the moths are absent or not available in numbers sufficient for bears to forage on them reliably

(Bjornlie and Haroldson 2008). Bears do not use all known moth aggregation sites in all years, but most sites are used in most years when moths are available. Whether moth sites will be dynamic in space and change in location over time in response to environmental factors influenced by climate change is yet to be seen.

Moth aggregation sites, wherever they are found, are likely to be located in high elevations, in talus that provides the appropriate structural and thermal habitat for moths, and within some distance to nectar sources. The model presented here is generalizable throughout the GYE, the area for which it was developed. The inference from this model may be restricted to the climatic characteristics under which the model was created because climate may affect Landsat data. Some variables in this model such as elevation, geology and Landsat data, although they may not have the same relationships to moth and bear presence outside the GYE, still are likely to be important in areas outside the GYE. Projecting the model presented here into a new area would be limited by variables that may be classified differently in different areas (*e.g.*, geology), and perhaps Landsat data may have different signatures in different areas. For example, geology and wetness values may be different in other places where bears feed on moths such as Glacier National Park in northwestern Montana. Although the variables ruggedness, slope, aspect, and heat-load were each significant in the models in the GYE, they did not contribute much to drops in deviance. It is possible that these variables may have different relationships in other areas like Glacier National Park. Developing models of moth and potential bear habitat in different areas and examining their commonalities may provide more generalizable models. In a bear management context, however, models of moth and potential bear habitat that are specific to certain areas might be more

appropriate to managing distinct population segments of bears such as those in the GYE and Glacier National Park.

MANAGEMENT CONSIDERATIONS

The purpose of the *Conservation Strategy*, or its replacement, and the accompanying bear management plans of Idaho, Montana, and Wyoming are to provide a framework for grizzly bear conservation. These plans allow expansion of the grizzly bear population into biologically and socially acceptable areas beyond the PCA and mandate the use of georeferenced habitat data to identify and manage these areas.

Moth sites are remote and are scattered within the GYE, and most sites we know about are clustered in the northeastern part of the ecosystem. Biologists first discovered that these moth sites were used by bears via observation flights. In areas into which bears are expanding but are less common we cannot rely on bear sightings to indicate areas where moths occur. The model presented here can help forecast areas into which bears might expand within and beyond the PCA.

The model presented here provides a starting point with which to determine where moths might occur. This model is more specific than a model of moth habitat alone because the data used to generate the model are based on locations where bears feed on moths. Therefore the model may reflect sites that bears prefer to forage for moths more than the distribution of moths on the high elevation landscape. A model of moth habitat might predict more areas and, depending on the flexibility in which the bears search and use the landscape, could identify more areas bears could use.

Identifying these areas may both inform where potential conflicts might occur and provide information on how such conflicts might be avoided spatially at certain times of the year. White *et al.* (1999) found that bears using moth sites in Glacier National Park were sensitive to disturbance from back country users, specifically mountain climbers. When climbers were present, bears spent less time foraging, increased defensive behaviors during the disturbance, and in some cases climber activity displaced bears from sites (White *et al.* 1999). Bears that were displaced from sites did not return within the same day (White *et al.* 1999), and disturbed bears may flee up to 0.5 km before stopping (H. Robison, pers. observ.). Disturbance and displacement may reduce food intake (White *et al.* 1999). Disturbance and vigilance responses are likely influenced by the lack of hiding cover at moth sites.

The model I presented here may assist with managing potential conflicts as bears expand into new areas searching for moths. Various management scenarios may help minimize disturbance and human-bear conflict at or near moth sites. For example, closing or restricting use in certain areas during specific times of the year (*e.g.*, mid-July through September), providing information on where people might encounter bears as they expand their range, considering buffer zones of no or reduced activity around moth sites, and proposing alternative climbing routes and flight height restrictions over sites (White *et al.* 1999) may help minimize disturbance and potential human-bear conflict at or near sites.

Human-bear conflict often leads to human-caused bear mortality, and, therefore, proactive management both to reduce conflicts between humans and bears and to allow for their coexistence is essential to bear persistence. Decreasing bear population

trajectories triggered by human-caused bear mortality prompted the listing of the bear (Mattson *et al.* 1996). For the foreseeable future, balancing recruitment and mortality is the key to bear management and conservation in the GYE (Schwartz *et al.* 2006).

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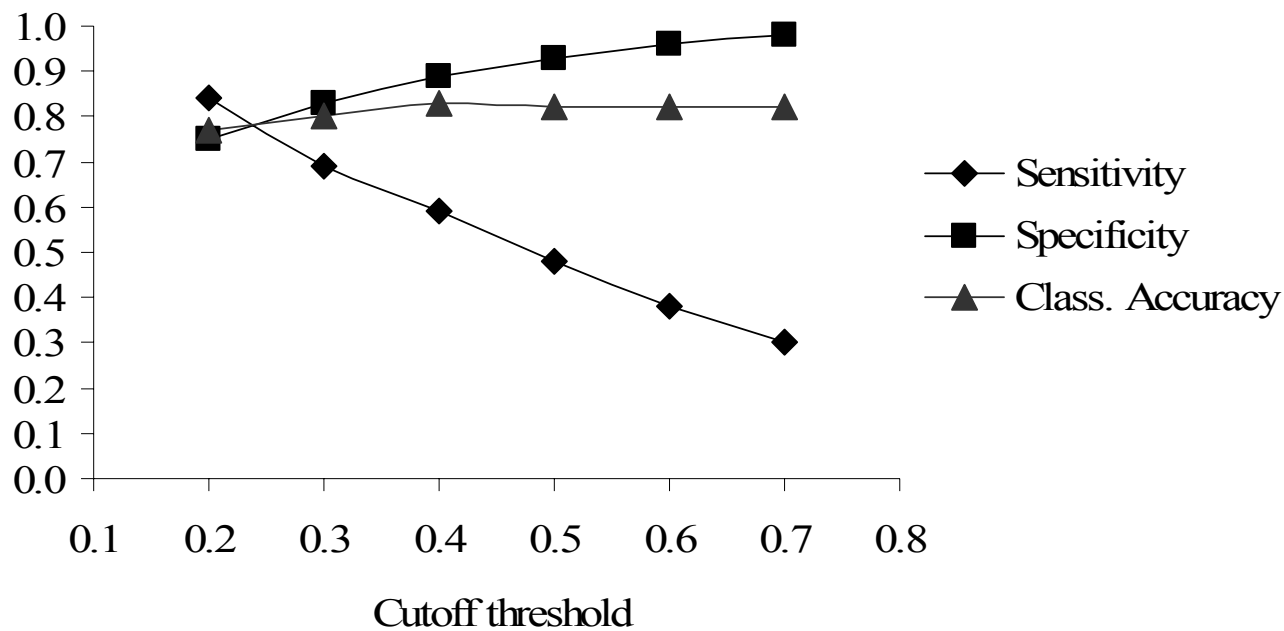


Figure 1. Model 2. The relationship of threshold cutoff with sensitivity, specificity and classification accuracy.

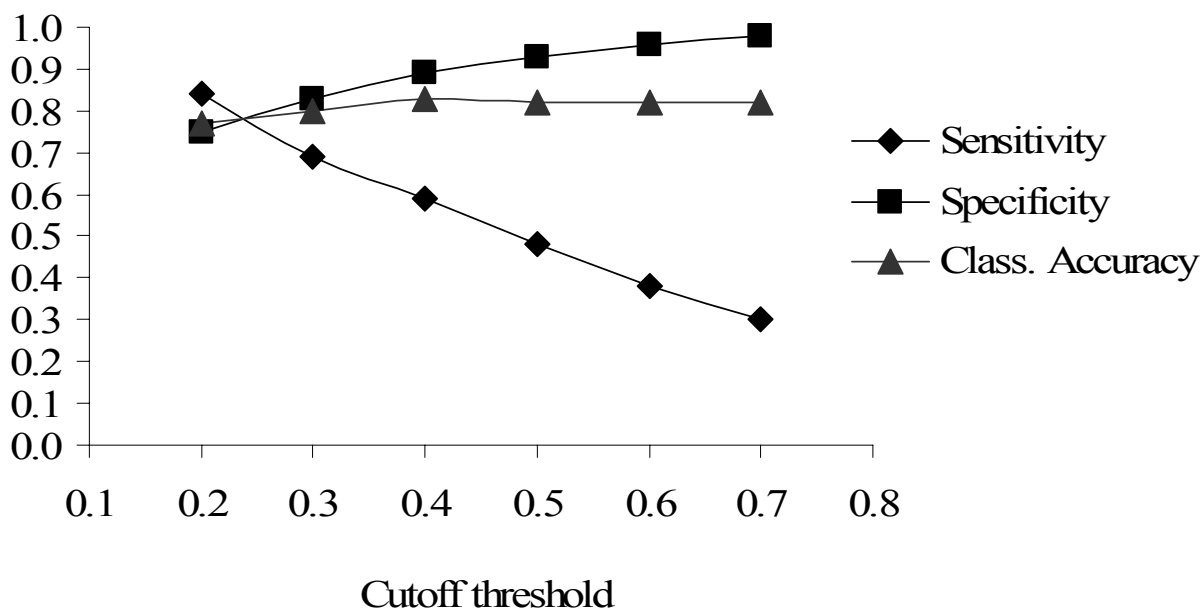


Figure 2. Model 3. The relationship of threshold cutoff with sensitivity, specificity and classification accuracy.

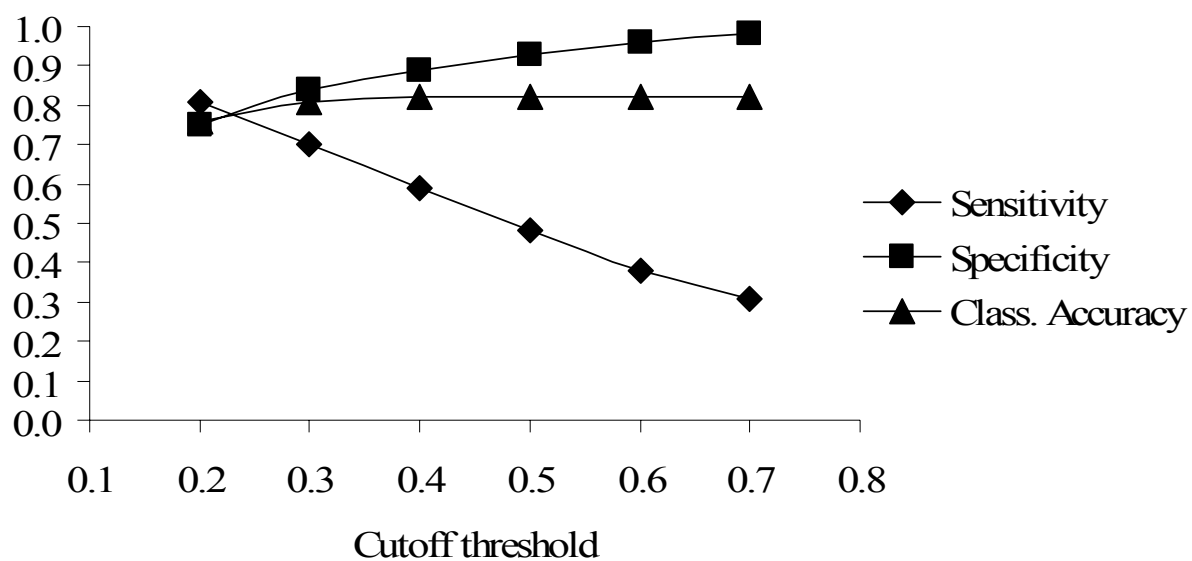


Figure 3. Model 4. The relationship of threshold cutoff with sensitivity, specificity and classification accuracy.

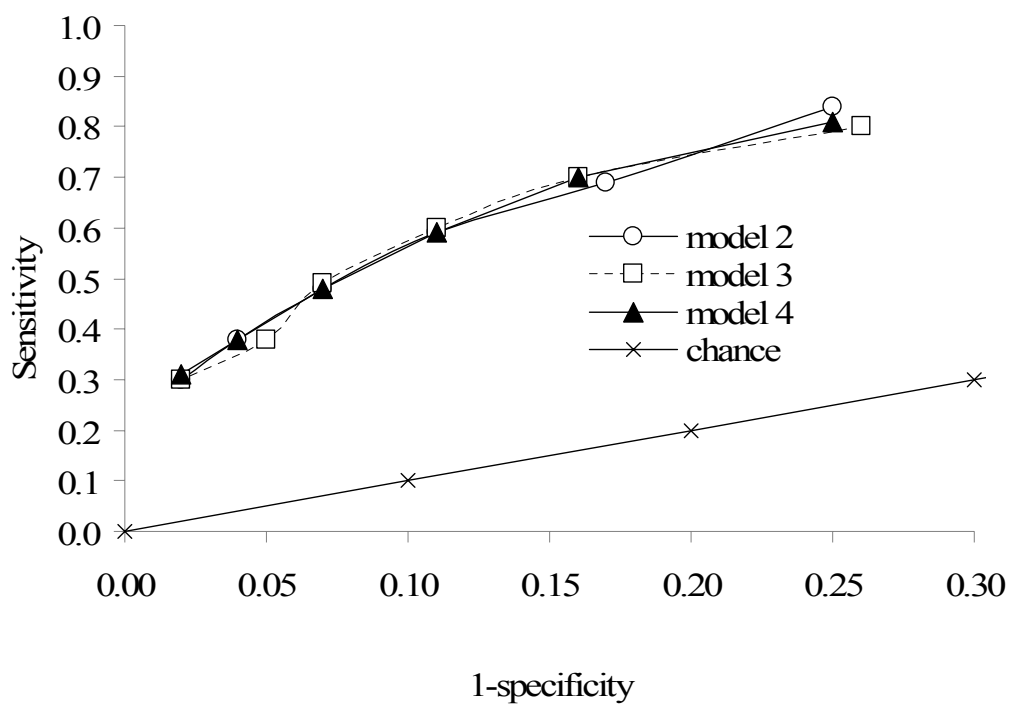


Figure 4. ROC plot of models 2 – 4. “Chance” indicates chance performance of the model (*i.e.*, not different from random expectation).

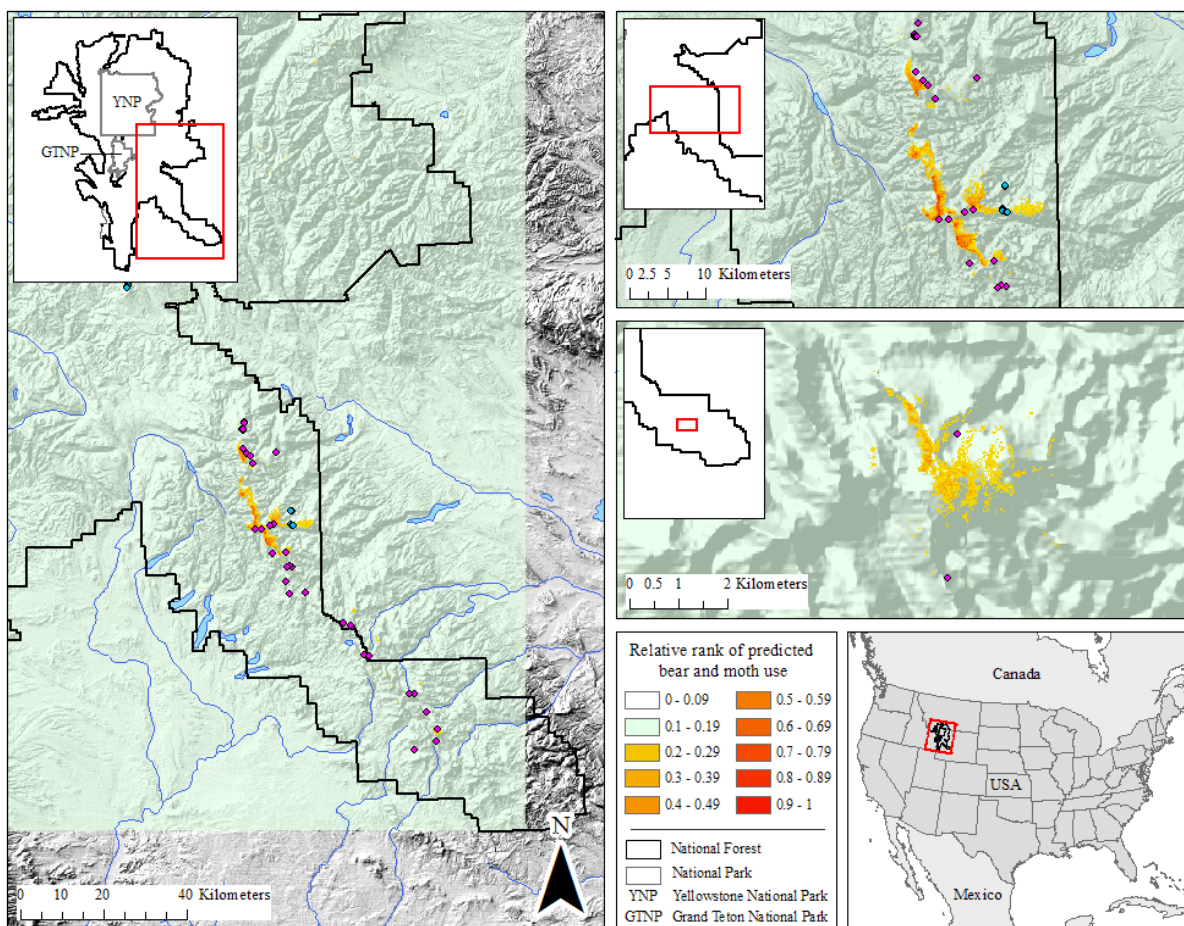
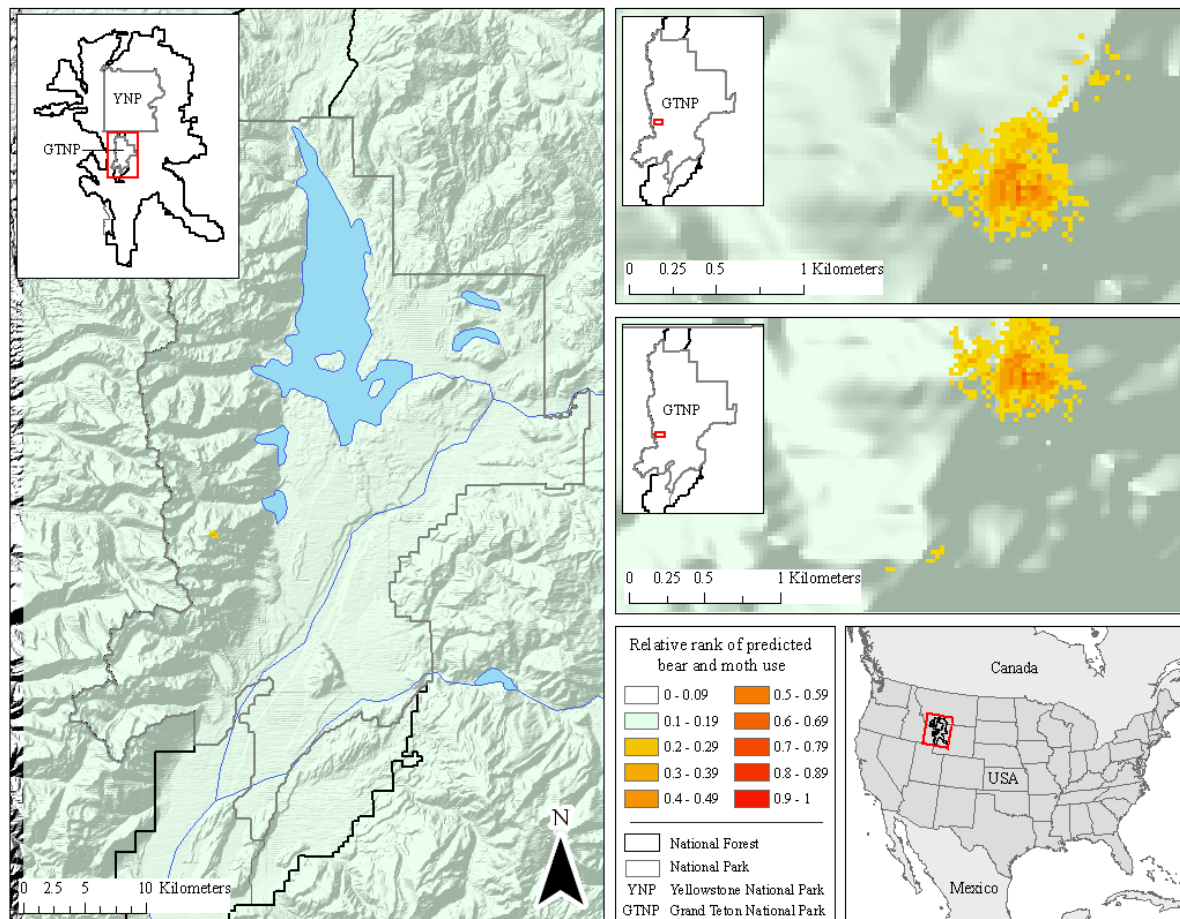


Figure 5. Map of model 4 in the Wind River Mountains including two areas of detail. Blue and purple points are sites that were visited to determine the presence of moths.



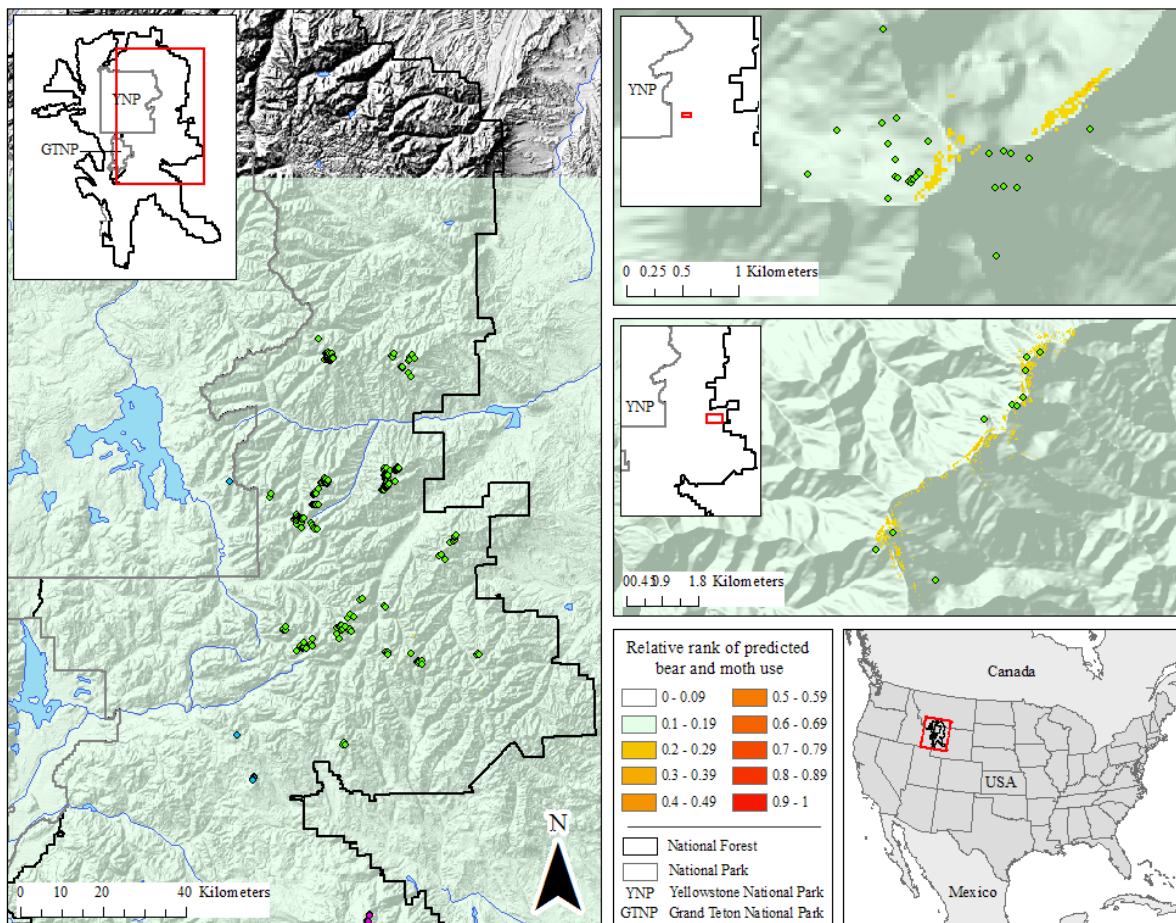


Figure 7. Map of model 4 in the Absaroka Mountains including two areas of detail. Green points are locations of bears foraging on moths. Blue and purple points are sites that were visited to determine the presence of moths.

Table 1. Environmental variables used to develop models of high elevation moth and bear habitat in the GYE.

Variables	Details	References
Elevation	Elevation extracted from 30 m digital elevation model	ArcMap 9.2, Intersect Point Tool (Hawth's Analysis Tools version 3.27© 2002-2006)
Elevation-sd	Standard deviation of elevation	
heat-load	A index of heat-loading of terrain	McCune and Keon 2002, Parks 2004 (ArcScript)
heat load-sd	Standard deviation of heat-load	
EW aspect	Aspect linearized via $\cos((\text{aspect}-90) * \pi/180)$ to represent the E-W component	ArcMap 9.2, Aspect tool, Raster Calculator
EW aspect-sd	Standard deviation of EW aspect	
NS aspect	Aspect linearized via $\cos(\text{aspect} * \pi/180)$ to represent N-S component	ArcMap 9.2, Aspect tool, Raster Calculator
NS aspect-sd	Standard deviation of NS aspect	
ruggedness	An index of the difference in elevation between adjacent cells of a digital elevation grid	Riley <i>et al.</i> 1999, Evans 2004 (ArcScript)
ruggedness-sd	Standard deviation of ruggedness	
Slope	Rate of change between each cell and its neighbors	ArcMap 9.2, Slope tool
slope-sd	Standard deviation of slope	
Profile	The rate of change in slope	ArcInfo 1982-2006
profile-sd	Standard deviation of profile	
planimetry	Planimetric change along contours (<i>e.g.</i> , gullies, ridges)	ArcInfo 1982-2006
planimetry-sd	Standard deviation of planimetry	
brightness	Landsat TM pixels of tasseled cap brightness	Crist <i>et al.</i> 1986, ENVI 2008
brightness-sd	Standard deviation of brightness	
greenness	Landsat TM pixels of tasseled cap greenness	Crist <i>et al.</i> 1986, ENVI 2008
greenness-sd	Standard deviation of greenness	
Wetness	Landsat TM pixels of tasseled cap wetness	Crist <i>et al.</i> 1986, ENVI 2008
wetness-sd	Standard deviation of wetness	
Principal components	Landsat TM pixels of principal components 1-6	ArcMap 9.2, Principal Components tool
Principal components-sd	Standard deviation of principal components 1-6	
surficial geology	Surface geology: landslides, bedrock, residuum, slopewash, colluvium, glaciated, glacial deposits	Case <i>et al.</i> 1998

Table 2. Models selected for testing.

model 1	elevation + heat load + roughness + wetness + greenness + EW aspect + geology
model 2	elevation + heat load + roughness + principal component 2 + EW aspect + geology
model 3	elevation + heat load + slope + principal component 2 + EW aspect + geology
model 4	elevation + heat load + slope + wetness + greenness + EW aspect + geology

Table 3. Final models based on AIC scores and χ^2 drop-in-deviance tests.

model 1	elevation + wetness + EW aspect + geology
model 2	elevation + heat load + roughness + principal component 2 + EW aspect + geology
model 3	elevation + heat load + slope + principal component 2 + EW aspect + geology
model 4	elevation + heat load + slope + wetness + greenness + EW aspect + geology

Table 4. Models and evaluation measures.

Model	AIC	Δ AIC	D^2_{adj}	K_{max}
Model 4	986.60		0.32	0.50
Model 2	990.86	4.26	0.31	0.50
Model 3	991.61	0.75	0.31	0.50

Table 5. Coefficients, their standard errors, odds ratios, their 95% confidence intervals, and significance for the best model, model 4.

Model	Variable	β	SE	Odds ratio	CI lower	CI upper	P
Model 4	elevation	0.0061	0.0006	1.0100E+00	1.0050E+00	1.0100E+00	0.0000
	heat-load	0.9145	0.2932	2.5000E+00	1.4000E+00	4.4300E+00	0.0000
	slope	0.0415	0.0008	1.0000E+00	1.0000E+00	1.0100E+00	0.0000
	wetness	0.0071	0.0013	1.0100E+00	1.0000E+00	1.0100E+00	0.0000
	EW aspect	-0.3854	0.1518	6.8000E-01	5.0500E-01	9.1600E-01	0.0008
	glaciated	-2.7289	0.7833	6.5300E-02	1.4100E-02	3.0300E-01	0.0000
	glacial deposits	0.6001	0.3826	1.8200E+00	8.6100E-01	3.8600E+00	0.0000
	landslides	-0.4631	0.2429	6.2900E-01	3.9100E-01	1.0100E+00	0.0000
	bedrock	-1.4425	0.2043	2.3600E-01	1.5800E-01	3.5300E-01	0.0000
	residuum	-2.3977	0.3101	9.0900E-02	4.9500E-02	1.6700E-01	0.0000
	slopewash	-2.4893	1.0972	8.3000E-02	9.6600E-03	7.1300E-01	0.0000

CHAPTER 5

Looking back at army cutworm moth ecology and looking forward to grizzly bear conservation

INTRODUCTION

In the preceding chapters I discuss various aspects of army cutworm moth (*Euxoa auxiliaris*) ecology and its interface with grizzly bear (*Ursus arctos horribilis*) conservation. The moths are native to North America, and during their one-year lifespan they are both agricultural pests in the Great Plains and Intermountain West and an important food for grizzly bears in the high alpine of the Rocky Mountains (Pruess 1967, Mattson *et al.* 1991, French *et al.* 1994, White *et al.* 1998a,b). Other species feed on the moths as well, and the moths pollinate alpine plants (French *et al.* 1994, Kevan and Kendall 1997). Studies of the moth in its low and high elevation habitats have been conducted largely independently by entomologists and wildlife ecologists; interdisciplinary studies are rare. My goals in this chapter are to synthesize the preceding chapters, which have been interdisciplinary, and to propose ways in which we might better understand moth ecology and the availability of moths to grizzly bears in light of what I presented in earlier chapters.

RESULTS

Chapter 1 – literature review

In Chapter 1 I review and synthesize information about *E. auxiliaris* taxonomy, life history, and the moths' importance to bears. *E. auxiliaris* is a member of the Noctuidae, the largest family within the order Lepidoptera. It is a widespread species, and it inhabits both open arid lands and forested areas (Lafontaine 1982). The genus *Euxoa* is highly diverse and in North America may eventually comprise approximately 200 species (Hardwick 1970). The genus is a difficult one on which to work because there are few structural characters by which species can be distinguished (Hardwick 1970). Additionally, there is evidence of interspecific hybridization within the genus (Hardwick 1970). Both of these facts may suggest that the genus is in “a state of great evolutionary mutability” (Hardwick 1970).

With the advent of agriculture in low elevation areas within the moth's range, it has become an agricultural pest (Strickland 1916, Burton *et al.* 1980). The moth feeds on a variety of native and introduced plants ranging from grasses (*Poa* spp.) to beets (*Beta vulgaris*). Larvae usually do not kill plants but do stunt their growth. Farmers, therefore, accept a certain level of damage to their crops (Blodgett *et al.* 2003) before applying pesticides to control larvae.

Moths migrate from low elevations in the Great Plains and Intermountain West to high elevations in the Rocky Mountains during the summer (Pruess 1967). Although biologists who have studied *E. auxiliaris* to date agree that temperature (Pruess 1967, Hardwick and Lefkovitch 1971, Oku 1983) and aridity (Hardwick and Lefkovitch 1971, Oku 1983) may motivate the migration, the physiological and ecological mechanisms that actually trigger

migration remain unknown. While the moths are in high elevations they feed on nectar at night and hide in talus during the day (French *et al.* 1994, O'Brien and Lindzey 1994). The moths may seek certain microsites within the talus (White *et al.* 1998b) near snowfields or meltwaters (French *et al.* 1994). The moths become reproductively mature (*i.e.*, they call with a pheromone and mate) in high elevations. The moths were thought to meet the expectations of “oogenesis syndrome” (Johnson 1969, Kevan and Kendall 1997). This syndrome stipulates that migration and reproductive development are physiologically incompatible. Recent findings show that while the moths conform to this syndrome during their spring migration they do not during their flight in the autumn.

Most other migratory noctuids in North America migrate latitudinally (e.g. *Agrotis ipsilon* [Showers *et al.* 1993], *Helicoverpa zea*, *Spodoptera frugiperda* [Westbrook 2008], *Pseudaletia unipuncta* [McNeil *et al.* 1995]). Discerning latitude involves sun and celestial and geomagnetic compasses and appears to be easier for migrants than discerning longitude (Akesson and Hedenstrom 2007, Gould 2008). *E. auxiliaris* migrates longitudinally, but how the moths determine longitude is unknown.

The moths return to low elevations in the autumn. To power their migration they may use fat stores they accumulate in high elevation (White *et al.* 1998b), nectar sources available at that time of year (e.g. rabbit brush [*Chrysothamnus* spp.]) (Cook 1927), or use very little energy but instead rely on prevailing winds (K. Pruess, unpub. data).

Migrating moths apparently do not have fidelity to specific high or low elevation areas (H. Robison, Chapter 2). However, there are high elevation sites at which moths occur somewhat consistently across years, and when the moths are present bears visit these sites and feed on moths (Bjornlie and Haroldson 2008). Byers *et al.* (1987)

suggested that the moths may not always return to areas of their origin, and Pruess (1967) suggested that the moths could constitute a continuous gene pool based on the fact that he found no clines in the morphology of moths collected from the Great Plains west to the Rocky Mountains. Additionally, Hardwick and Lefkovitch (1971) suggested that the Rocky Mountains may not be a barrier to migration for various species of *Euxoa* based, in part, on the observations that similar associations of sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus* spp.), and ponderosa (*Pinus ponderosa*) or pinon (*Pinus monophylla*) pine are home to the same assemblages of species within the genus.

In the 1950s both scientists (Chapman *et al.* 1955) and outfitters (French *et al.* 1994) observed grizzly bears feeding on moths in talus at high elevations. Grizzly bears excavate the moths from talus and consume them by the millions from July through September (French *et al.* 1994, White 1996, White *et al.* 1998b, 1999). A grizzly bear can consume 40-60,000 moths in a day, and over a 30-day period a grizzly bear feeding extensively on moths can consume close to half of its yearly energy needs (White 1996, White *et al.* 1999). Moths, at 8 kcal/g, are the richest food available to grizzly bears in the Greater Yellowstone Ecosystem (GYE) (Mealey 1975, Pritchard and Robbins 1990, French *et al.* 1994). Moths also are available to the bears during hyperphagia (Mattson *et al.* 1991, French *et al.* 1994), an energetically demanding time of year for bears that lasts from mid-July until denning and during which the bears need to accumulate fat for hibernation (Nelson *et al.* 1980). O'Brien and Lindzey (1994) estimated that approximately 45% of GYE grizzly bears used moth sites. However, this proportion may be biased high because bears at moth sites may be more conspicuous than bears in other habitats (but see French *et al.* 1994). Moths also are eaten by a variety of other

mammals, birds, and invertebrates (French *et al.* 1994, White *et al.* 1998b, H. Robison, pers. observ.).

Moths and whitebark pine (*Pinus albicaulis*) are especially important to bears because they not only are rich in energy, but they also are available to bears in the autumn at high elevations. When bears move to high elevations to forage on these foods, they geographically separate themselves from areas of human activity. When autumn foods are scarce bears search widely for food and get into more conflicts with humans (Haroldson *et al.* 2006). Human-caused bear mortality is the major cause of death of bears in the GYE, and most of these deaths occur in the autumn (Haroldson *et al.* 2006). Additionally, there is a positive relationship between pine seed abundance and bear litter size (Mattson *et al.* 1992). Although there are no data available to test whether this relationship also exists with moths, scientists believe that moths may influence reproduction and survival of a segment of the bear population in the GYE (Schwartz *et al.* 2006). Balancing recruitment and mortality is the key issue in grizzly bear management and conservation in the GYE (Schwartz *et al.* 2006). Facilitating this balance includes understanding these foods better and educating the public on how to minimize conflicts with bears, especially when these foods are low in abundance.

Chapter 2 – moth population genetics and migration

In Chapter 2 I analyzed variation at microsatellite loci to understand gene flow in moths so I might describe more clearly both their migration and the scale at which it may influence their availability to bears.

Similar to other studies of species within the Lepidoptera (Ji and Zhang 2004, Zhang 2004), I had a low success rate of obtaining microsatellite loci from microsatellite libraries (5%). Additionally, I found evidence for microsatellite families, groups of non-coding genes with similar or identical repetitive flanking regions, in the moths. This may indicate that microsatellites are in an early stage of evolution in this taxon (Zhang 2004). This finding may corroborate the suggestion based on morphology that the genus is in “a state of great evolutionary mutability” (Hardwick 1970).

Analysis of variation at microsatellite loci indicates that moths from various locations within their range and from either side of the Continental Divide interbreed. This result supports the suggestions that the moths may constitute a continuous gene pool (Pruess 1967), the moths may not return to areas of their origin (Byers *et al.* 1987), and the Rocky Mountains may not be a barrier to migration for various species of *Euxoa* (Hardwick and Lefkovitch 1971). The moths’ migration has been studied westward to the Rocky Mountains from the east (Pruess *et al.* 1967); the findings I report indicate the moths also migrate to the Rocky Mountains from the west.

The finding that the moths that migrate to high elevations do not comprise unique subpopulations is important both to the persistence of the ecological relationship between grizzly bears and moths and to grizzly bear conservation in the Rocky Mountains. Bear conservation is facilitated when bears, seeking lipid-rich foods like whitebark pine seeds and moths, use remote, high elevation habitats that are relatively secure from conflicts with humans. High gene flow among moth populations suggests that local perturbations in one or a subset of the moths’ winter habitats (*e.g.*, from pesticide use, habitat conversion) will not result in the moths’ absence from specific high elevation sites.

Significant population structure, indicative of site fidelity, would make the moths highly susceptible to local perturbations at low elevations and likely result in corresponding extirpations at high elevation sites.

Chapter 3 – pesticide residues in moths and potential consequences to foraging bears

It is well-known that potentially toxic elements and chemicals can persist in environments and bioaccumulate in organisms (Kelly *et al.* 2004). Long distance transport of elements and chemicals from low to high elevations has been reported for alfalfa webworm moths (*Loxostege cereralis*) in North America, Bogong moths (*Agrotis infusa*) in Australia, and other insects (Halfpenny 1994, Green *et al.* 2001). *A. infusa* and *E. auxiliaris* have similar ecologies. *A. infusa* moths contain arsenic, which they transport from low to high elevations where pygmy possums, a major predator of the moths, consume it (Green *et al.* 2001).

Because grizzly bears consume millions of *E. auxiliaris* moths, there was concern about potential transport of pesticides that could bioaccumulate in bears (French *et al.* 1994). At the time of the study I reported in Chapter 3, carbamate, organophosphate, and pyrethroid chemicals were listed for controlling moth larvae in the states of Idaho, Montana, Nebraska, South Dakota, and Wyoming. Montana also recommended the use of two organochlorine pesticides. Some of these pesticides could potentially bioaccumulate and be physiologically toxic to bears. Therefore, in Chapter 3, I investigated whether moths contained pesticide concentrations sufficient to reach physiological toxicity in grizzly bears and whether moths transported pesticides to high elevations where grizzly bears forage for them.

The results of this study indicate that moths do not transport biologically significant (*i.e.*, physiologically toxic) levels of contaminants to high elevations and minimize concerns about chemical bioaccumulation in bears under current pesticide use. The low to undetectable levels I reported are logical because moths produce most of their fat body in the alpine where pesticides are not used. However, pesticide use remains relevant to bear conservation. When compared to domestic species typically used to determine chemical toxicities, bears have unique physiology including hyperphagia, brown fat accumulation, and torpor. This could result in differences in their assimilation or excretion of certain chemicals, particularly those stored in fat.

Chapter 4 – models of army cutworm moth and grizzly bear habitat

The U.S. Fish and Wildlife Service's (USFWS) *Conservation Strategy* for grizzly bear in the GYE was, until September 2009, the guiding document for the bear's conservation since its delisting in 2007 (USFWS 2007a, 2007b). The *Conservation Strategy* allowed bears to expand into biologically suitable and socially acceptable areas within and beyond the Primary Conservation Area (PCA) prescribed for the bear. It also mandated the use of georeferenced data to aid in monitoring the four major bear foods (moths, cutthroat trout [*Oncorhynchus clarki*], whitebark pine seeds, and winter-killed ungulates [*Bison bison*, *Cervus elaphus*, *Alces alces*, *Odocoileus hemionus*]) in the GYE and to identify habitats into which bears may expand (USFWS 2007a). In September 2009, a judge in Montana ruled in favor of relisting the bear, and federal protections have been reinstated (USFWS 2009). Therefore, the *Conservation Strategy* is no longer the guiding document for bear conservation. That being said, identifying potentially suitable

habitat for bears and monitoring critical bear foods will remain important to managing bears, and managers will need to know where bear foods occur or might occur.

In Chapter 4 I described high elevation habitat used by moths and grizzly bears in the GYE using a dataset of locations where bears feed on moths and a random sample of available habitat encompassing all sites where bears forage on moths. My goal was to model the spatial probability of occurrence of both moths and the interspecific interaction between bears and moths. Additionally, I aimed to create a tool with which biologists and managers can identify habitat that moths and bears may use within the PCA and that bears can expand into to forage on moths beyond the PCA.

Habitat models indicated that elevation, surficial geology, and “tassled cap wetness” derived from Landsat TM imagery describe areas used by moths and bears. In the best model, elevation caused the largest drops in deviance, followed by geology and wetness. Slope, aspect, and heat-load each also were significant and contributed to AIC values, but they did not contribute as much to drops in deviance. Glacial outwash, which may comprise talus, was positively associated with predicted presences with respect to the reference category colluvium (*i.e.*, loose rock that collects at the base of slopes). Landslides, bedrock, residuum, slopewash, and glaciated areas, were negatively associated with predicted presences with respect to colluvium.

Although measures of agreement between the data and the model predictions (K_{\max}) were moderate to good, the explained deviance (D^2_{adj}) and model sensitivities were a bit low. However, I visually inspected the maps resulting from the model with respect to sites that were visited and inspected for the presence of moths, and this revealed that the models perform fairly well qualitatively to indicate the general areas that we know moths

and bears currently use within the PCA. The model also predicts use areas near areas that bears are not currently using. The model also predicts areas where interactions between these species may occur outside the PCA in the Wind River and Teton Mountain Ranges into which bears are expanding.

Next steps

The ecology of *E. auxiliaris* is unusual for a noctuid moth in North America. Studying its ecology will continue to be challenging and likely will require the integration of a variety of different techniques. In the preceding chapters, I have used genetics, pesticide residue analysis, and habitat modeling to understand the moth's ecology and its relationship to grizzly bears more completely. In the following text, I recommend paths forward based on those findings.

The moths are reproductively active in both the alpine zone and in low elevations in the late summer and early autumn. The moths are panmictic or very nearly so and do not form different subpopulations based on their origins. Therefore, extirpations of moths in certain low elevation areas are not likely to result in extirpations at high elevation sites. Additionally, the moths appear to migrate to the Rocky Mountains from the west as well as from the east.

The moths do not contain or transport levels of pesticides that are biologically significant, so these compounds are unlikely to bioaccumulate in bears. Persistent chemicals I found in moths are at low levels and are now banned. Therefore, these chemicals will decrease in amount in the environment and in moths over time. However, because available pesticides and their listed uses change, I recommend repeating this work

in the future. I also recommend collecting and analyzing grizzly bear tissue for pesticide residues. These analyses should be performed on grizzly bear fat, blood, or hair taken from bears suspected of feeding at moth sites. Care must be taken to eliminate alternative sources of pesticides as they could confound residue levels attributable to moths. Additionally, if synergisms between the pesticides that are used are discovered, future studies will need to consider their effects.

The habitat models I developed and evaluated indicate that elevation, surficial geology, and wetness are important descriptors of sites used by moths and bears. Measures of agreement were good between the data and the best model's predictions despite the fact that the explained deviance was low. This could have been caused by the omission of variables that might be important but were not included in models because they have not been measured. Most ecological associations are not random but are spatially correlated because they occur in patches geographically (Legendre 1993). Including a variable that incorporates the spatial correlation of features that associate with moth and bear use may help improve model fit. Another factor that might influence use by moths and bears is the presence of snowfields and/or streams (French *et al.* 1994, H. Robison, pers. observ.) because they may influence the temperature gradient that moths seek (White *et al.* 1998b). Additionally, major drainage basins that orient E-W may funnel migrating moths toward sites. Another variable that is hard to assess other than from the ground is the character of the interstitial space of the talus. If the interstitial space of the talus is filled in it might not provide the right environment for moths. Additionally, moths release pheromone and mate in high elevations, and this might contribute both to moth site selection and moth aggregation in talus. It is also possible the bears locate moths in the

talus by scent. Also, the spatial relationship between nectaring areas and talus may influence moth use of sites. For example, there may be a distance beyond which moths do not travel between talus refugia and nectar sources. I recommend ground-truthing the model. If the model is not useful I recommend refining it by including the above variables, where available, and gathering information on the variables for which we do not currently have data.

The habitat model I developed is more specific than a model of moth habitat alone because the data used to generate the model are based on locations where bears feed on moths. Therefore the model may reflect areas where bears prefer to forage for moths more than distribution of moths on the high elevation landscape. A model of moth habitat might predict more areas and, depending on the flexibility in which the bears search and use the landscape, could identify more areas bears could use.

The ecological relationship between moths and bears is influenced by a number of factors including weather patterns that influence moth numbers in low elevations, the migration of moths to and their abundance in high elevations, the flower resources available to moths, the availability of talus and its thermal and structural characteristics, the securing of moth sites from disturbance, and potentially the availability of other foods during the time moths are available to bears. Thus, moth ecology and moth availability to bears are both influenced by events spanning both large temporal and spatial scales. These facts make it difficult to determine at which points important factors influence the continuum of moth recruitment to their presence at high elevation sites. A trapping program exists in Montana and other states in the High Plains that forecasts potential outbreaks of larvae in the spring (Blodgett *et al.* 2003). The forecast helps farmers decide

whether it is important economically to apply pesticides to their crops in the spring. The large-scale inventory on moth abundance stops after the autumn trapping session that produces the spring forecast (Figure 1).

While the moth monitoring and forecasting currently conducted in low elevations suits the needs of farmers, it falls short of the needs of grizzly bear managers. A strategy useful for bear conservation might involve forecasting the number of moths that leave low elevations en route to high elevations where they may become bear food. It would be useful for entomologists and wildlife managers to collaborate on a system to monitor moth migration. A monitoring system such as this would require techniques from various disciplines. Currently, progress in migratory ecology is encouraging and uses techniques that span disciplines from physiology and ecology (McNiel *et al.* 1995, Gould 2008) to meteorology and includes direct (e.g. aerial nets, airplanes) and indirect (e.g. X-band radar, NEXRAD Doppler radar) methods (Westbrook 2008).

Conceptual models can help identify the information that biologists need to understand ecological systems more clearly. In Figure 1 I describe a conceptual model that identifies points at which data can be collected to link the forecast of moth numbers in the spring with a summer forecast of the number of moths (or an index of that number) that might reach high elevation sites. The summer forecast would have to incorporate the predicted number of moths from the spring forecast with the intensity of control method used (*e.g.*, heavy pesticide application, light pesticide application, none) and the number of larvae that survive both to pupate and to become moths. Environmental factors including degree days and moisture/precipitation also will influence this (Figure 1, items 12 and 14). Wind also may influence the numbers and timing of moths reaching high elevation areas.

Once moths reach high elevation areas, talus habitat needs to be available (*i.e.*, free from snow) for them to aggregate within it and be available to bears. A model that aims to forecast moth availability to bears could include a measure of snow cover at aggregation sites. Since *E. auxiliaris* is a widespread species that inhabits arid lands and forested areas (Lafontaine 1982), the moths may seek shelter in trees near the tree line below the talus. Moths have been found wedged in various objects at or below tree line (H. Robison, pers. observ.). The model proposed in Figure 1 incorporates a variety of factors, requires a new data collection regime, and could be difficult carry out. A simpler method could involve investigating relationships between past forecasts of larvae in the spring, the intensity of control used on larvae (*i.e.*, amount of pesticide application, if available), the number of moth sites used by bears, and the number of bears seen foraging at moth sites. Additionally, because moths are panmictic, or nearly so, they are likely coming from many different locations over a very large low elevation area. Thus, a moth trapping program conducted at critical migratory locations (*e.g.*, “pinch points” in topography) could be used to establish an index of moth abundance or availability to bears. The model I presented in Chapter 4 of high elevation habitat used by moths and bears indicates that these sites likely are spread widely throughout the GYE. This habitat model can be used to help design high elevation trap stations that could be sampled in concert with trap stations at “pinch points” at lower elevations.

Collecting the information indicated in Figure 1 would both fill the gaps in our knowledge of moth ecology and migration and help forecast moth availability to bears and facilitate bear conservation. When autumn foods are scarce bears get into more conflicts with humans, and most human-caused bear mortalities occur in autumn (Haroldson *et al.*

2006). Autumn foods are also important to recruitment. Specifically, pine seed abundance correlates with larger litter size of bears (Mattson *et al.* 1992). Moths may influence reproduction and survival of a segment of the bear population in the GYE (Schwartz *et al.* 2006), but currently there are no data to test this. There is a method managers use to monitor whitebark pine seeds and to forecast seed availability to bears in the GYE, and managers would like to develop a system with which to monitor moths (Schwartz *et al.* 2006). For example, in years where pine seeds are forecasted to be low, managers can use this information to alert the public both that bears will be foraging widely and seeking alternative foods and that people need to be more vigilant about securing attractants (*e.g.*, game meat storage) and human foods away from bears. These measures help minimize conflicts between humans and bears that can be fatal for bears.

A moth monitoring system would allow managers to respond in a similar way as when pine seeds are forecasted to be low, and more importantly, when both of these foods are predicted to be low. Additionally, whitebark pine is threatened both by blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) (Reinhart *et al.* 2001, Haroldson *et al.* 2003). These threats will influence the abundance of pine seeds. It is possible that there could be compounding effects on food scarcity at high elevations when both pine seeds and moths are low in abundance.

Climate change is large-scale factor that might influence the abundance of moths over time, the ecological relationship between moths and bears, and a monitoring system for moths. Warming and drying in low elevation areas, might influence the timing of moth migration to high elevation areas. Temperature and aridity are related to the moths' migration (Pruess 1967, Hardwick and Lefkovitch 1971, Oku 1983). Currently, in southern

latitudes within the moth's range, the moths migrate to the mountains earlier in the summer/spring and return to low elevations later in the autumn (Oku 1983). At higher latitudes within the moths range they cease to migrate (Oku 1983). It is possible that as climate warms the timing of the interaction between moths and bears may shift.

Alternatively, if climate change results in precipitation regimes that cause wet springs in low elevation areas within the moth's range larvae will drown. This would decrease moth recruitment and the number adults that migrate to high elevations. In high elevations, climate change likely will influence the community of flowers available to moths at high elevations. Moths, however, do not appear to be specialists (H. Robison, unpub. data) and may be able to switch to other flowers as they expand upslope and replace existing plants. A more limiting factor on the suitability of moth habitat in high elevations likely will be the persistence of a temperature gradient within the talus that is provided by snow, ice, and meltwater.

The results of my research are relevant to the broader ecological roles of moths. Understanding moth origins, chemical loads in moths, and moth habitat is necessary to understand the moth's relationship to other animal and plant species and potentially to nutrient fluxes in high elevation ecosystems. A suite of predators other than grizzly bears forage on moths, including black bears (*Ursus americanus*), coyotes (*Canis latrans*), bats, mice, mustelids (species not identified) (French *et al.* 1994, White *et al.* 1998b, H. Robison, pers. observ.); ravens (*Corvus corax*), American pipits (*Anthus rubescens*), mountain bluebirds (*Sialia currucoides*), gray-crowned rosy finches (*Leucosticte tephrocotis*), black rosy finches (*Leucosticte atrata*), Clark's nutcrackers (*Nucifraga columbiana*) (French *et al.* 1994, White *et al.* 1998b); and wolf spiders (Lycosidae) (H.

Robison, pers. observ.). The moth's importance to these species and potentially to other species has yet to be studied. Some species may be, like the gray-crowned rosy-finch, species of concern. Moths pollinate a variety of alpine plants (Kevan and Kendall 1997) and they may provide an important role in maintaining alpine floral communities. Additionally, moths transport nutrients such as nitrogen between low and high elevation ecosystems (White 1996). Nitrogen influx is important to alpine ecosystems because it influences primary production of these areas (Bowman *et al.* 1993).

Finally, from a bear management perspective, understanding the availability of moths to bears using a variety of techniques over spatial and temporal scales in the context of a changing climate is important to bear conservation because the moths are high in energy and are located in areas relatively secure from humans. Balancing mortality and recruitment is key to grizzly bear conservation in the GYE (Schwartz *et al.* 2006). Management that minimizes conflicts between humans and bears is important not only within the PCA, but also beyond the PCA because areas outside the PCA have been implicated as a sink for bears (Schwartz *et al.* 2006). Cultivating human tolerance of bears and educating the public on how both to live with bears and to minimize human-bear conflicts within and beyond the PCA is critical to balancing mortality and recruitment (Schwartz *et al.* 2006). This will be even more important as areas used by bears and humans continue to overlap within and beyond the PCA.

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PERSONAL COMMUNICATIONS

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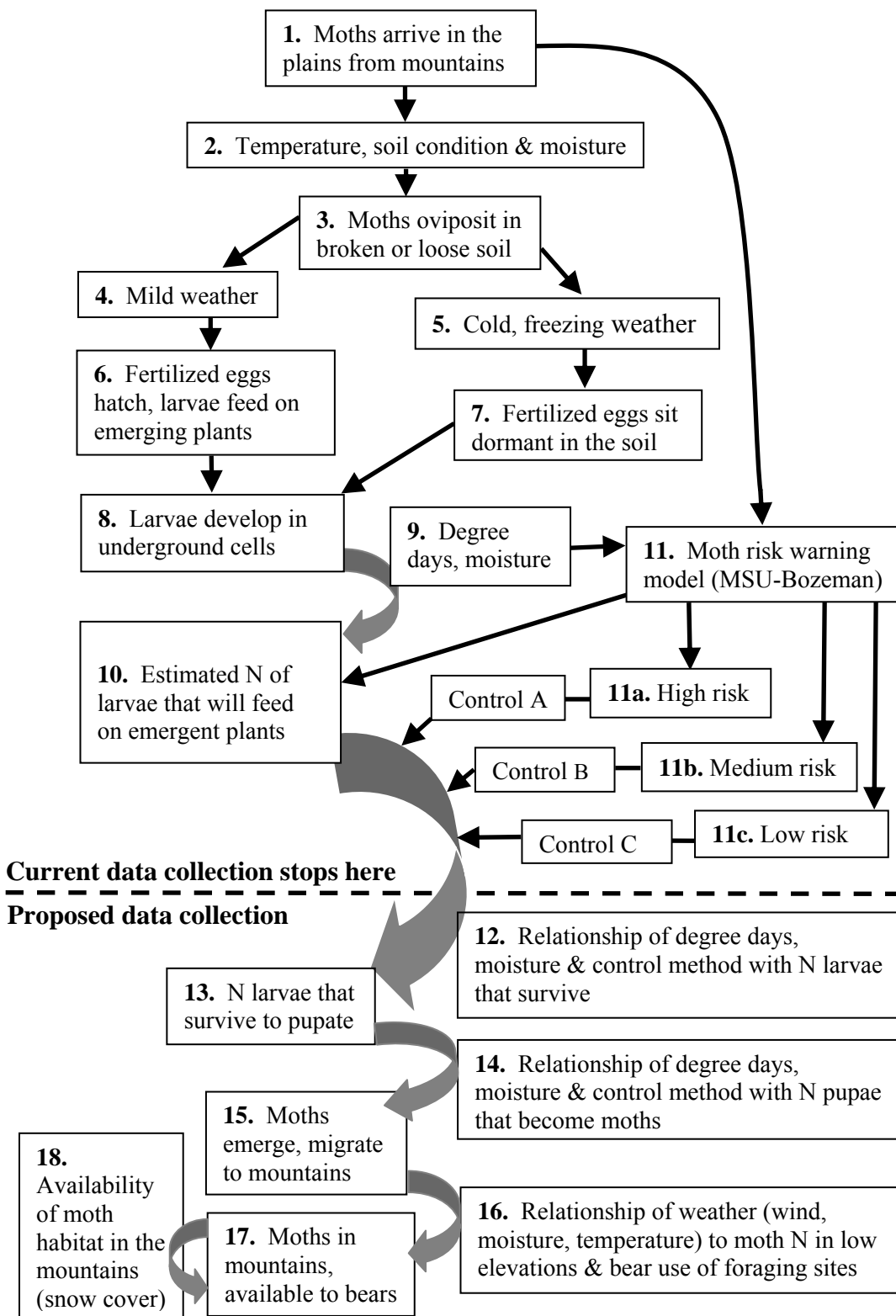


Figure 1. A conceptual model of moth ecology and the factors that likely influence it.