Coefficients of Productivity for Yellowstone's Grizzly Bear Habitat

By David J. Mattson,[1] Kim Barber,[2] Ralene Maw,[3] and Roy Renkin[4]

Abstract

This report describes methods for calculating coefficients used to depict habitat productivity for grizzly bears in the Yellowstone ecosystem. Calculations based on these coefficients are used in the Yellowstone Grizzly Bear Cumulative Effects Model to map the distribution of habitat productivity and account for the impacts of human facilities. The coefficients of habitat productivity incorporate detailed information that was collected over a 20-year period (1977–96) on the foraging behavior of Yellowstone's bears and include records of what bears were feeding on, when and where they fed, the extent of that feeding activity, and relative measures of the quantity consumed. The coefficients also incorporate information, collected primarily from 1986 to 1992, on the nutrient content of foods that were consumed, their digestibility, characteristic bite sizes, and the energy required to extract and handle each food. Coefficients were calculated for different time periods and different habitat types, specific to different parts of the Yellowstone ecosystem. Stratifications included four seasons of bear activity (spring, estrus, early hyperphagia, late hyperphagia), years when ungulate carrion and whitebark pine seed crops were abundant versus not, areas adjacent to (<100 m) or far away from forest/nonforest edges, and areas inside or outside of ungulate winter ranges. Densities of bear activity in each region, habitat type, and time period were incorporated into calculations, controlling for the effects of proximity to human facilities. The coefficients described in this report and associated estimates of grizzly bear habitat productivity are unique among many efforts to model the conditions of bear habitat because calculations include information on energetics derived from the observed behavior of radio-marked bears.

Introduction

The Yellowstone grizzly bear cumulative effects model (CEM) is used to assess the inherent productivity of grizzly bear habitat (see Appendix 1 for scientific names) and the impacts of human activities on bear use of that productivity potential (Weaver and others, 1986; Dixon, 1997). The CEM was developed by a team from the U.S. Forest Service and National Park Service in the mid-1980s in response to regulatory requirements that management agencies determine the cumulative effects of humans on grizzly bear populations listed under the U.S. Endangered Species Act (Dixon, 1997). Operations of the CEM can be characterized as those involved with data management, geographic information systems (GIS), and matrices of coefficients that are applied to map polygons on the basis of polygon attributes. One set of matrices is used to ascribe inherent habitat productivity to polygons, while another set of matrices is used to reduce that productivity depending on intersections of the habitat with "zones-of-influence" associated with human activities (see Appendix 2). Coefficients of inherent habitat productivity vary with the season, habitat type (e.g., Steele and others, 1983), vegetation cover type (Despain, 1990), proximity to forest/nonforest edge, occurrence in an ungulate winter range, occurrence near cutthroat trout spawning streams, and occurrence near sites where army cutworm moths aggregate (see Mattson and others, 1986; Mattson and Knight, 1989).

Coefficients of habitat productivity that were previously used in operations of the Yellowstone grizzly bear CEM were developed in 1984, a time when relevant data were limited or even unavailable (Dixon, 1997). Because of limited data, it was understood that habitat coefficients were to be used primarily to assess and refine model performance. It was further assumed by those involved in developing the CEM that coefficients suitable for model applications would be developed at some later date when more of the requisite data were available, allowing not only for greater sample sizes but also for improvement in methods.

Much of the data that were missing or sparse in the mid-1980s are currently available. Previous coefficients used in model operations were based on grizzly bear data collected from 1977 to 1983. Since then, the amount of relevant grizzly

---

[1] U.S. Geological Survey, Southwest Biological Science Center, Colorado Plateau Research Station, P.O. Box 5614, Northern Arizona University, Flagstaff, Arizona 86011-5614

[2] U.S. Forest Service, Shoshone National Forest, 808 Meadow Lane, Cody, Wyoming 82414

[3] U.S. Forest Service, Region 4, 324 25th Street, Ogden, Utah 84401

[4] National Park Service, P.O. Box 168, Yellowstone National Park, Wyoming 82190

bear data has more than tripled. More important, information was collected from 1986 to 1996 with the intent of remedying deficiencies identified during the calculation of coefficients in 1984. Many of the parameters arrived at by professional judgement in 1984 can now be estimated empirically. Similarly, digital maps for estimating the aerial extent of different habitat strata were available only for the Yellowstone National Park portion of the ecosystem or, for some features, were not available at all. This situation has changed dramatically. Digital data for all relevant map features, for the full extent of the Yellowstone ecosystem, are now available.

New data and new analytical methods led to a directive from the Yellowstone ecosystem's grizzly bear managers for researchers to recalculate matrices of coefficients used in the Yellowstone grizzly bear CEM for assessing inherent habitat productivity. This charge stemmed from a growing appreciation of the limits of historical coefficients and a desire to incorporate as much of the newer grizzly bear information as possible, using improved methods for calculations. The data and methods used to recalculate habitat coefficients for the Yellowstone ecosystem are described in this paper.

Objective

Our primary objective was to produce coefficients that can be (1) applied to currently mapped features of Yellowstone grizzly bear habitat and (2) used to calculate unit-area estimates of energy and nutrients derived by grizzly bears from specified map polygons. These estimates account for digestive efficiencies as well as certain energetic costs. The resulting map of relative unit-area net digested energy is roughly equivalent to a map of habitat capability or productivity. The "new" coefficients incorporate all of the available and relevant information from analyses of grizzly bear foraging activity conducted from 1977 to 1996 by the Interagency Grizzly Bear Study Team (IGBST). The IGBST was formed in 1973 and currently consists of the U.S. Geological Survey, National Park Service, U.S. Forest Service, and game management agencies from the States of Wyoming, Montana, and Idaho.

Other analyses of grizzly bear habitat use in the Yellowstone ecosystem have focused on estimating grizzly bear distribution with respect to explanatory features of their habitat, with an emphasis on the effects of human facilities (see Mattson and others, 1987, 1992; Mattson, 1997a). These analyses have not explicitly incorporated detailed information on grizzly bear foraging behavior and the associated gains or losses of energy and nutrients. The Yellowstone ecosystem is unique in having a large amount of this information available. Furthermore, the energetics of different activities, ranging from travel to consumption of high quality foods such as ungulate meat or seeds of whitebark pine, vary by orders of magnitude (Hamer and Herrero, 1987; Mattson, 1997a).

The primary response variable in this analysis is a time-specific index of net digested energy, rather than a time-specific probability of location. In this regard, other analyses have not focused on estimating the inherent "productivity" or "capability" of grizzly bear habitat, which is the primary aim of the approach described here. Although "productivity" is somewhat of an abstract parameter, it is foundational to operations of the CEM for grizzly bear habitat in the Yellowstone ecosystem. The CEM begins by calculating intrinsic habitat productivity and then reduces that value by varying degrees near human facilities or activities. In theory, this decrease in productivity value reflects reductions in "food availability" that are either a result of humans selectively killing bears that use human-influenced niches or of bears avoiding these same areas because they are wary of humans (Mattson and others, 1987, 1992, 1996; Pease and Mattson, 1999). Thus, the calculation of coefficients described here is tailored to grizzly bear habitat use and grizzly bear and human interactions as conceptualized in the Yellowstone CEM.

Methods

Field Methods

We obtained data from grizzly bears that were trapped and radio-marked in the Yellowstone ecosystem from 1975 to 1996. We located these marked bears from fixed-wing aircraft by aerial telemetry once to twice a week. Although trapping was done in a way that attempted to represent different parts of the Yellowstone ecosystem, it was not randomized, especially with respect to distance from roads. Some Bear Management Units (BMUs) were also undersampled because of low bear densities and/or low levels of trapping effort. See Knight and Eberhardt (1985) and Blanchard and Knight (1991) for detailed descriptions of trapping and telemetry location methods.

Triplet grizzly bear cubs (third cub is behind cub on right) on the Two Ocean Plateau of Yellowstone National Park. Although most grizzly bear females have litters of two cubs, females with access to abundant whitebark pine seeds more often have triplets (photo by Bart Schleyer, Interagency Grizzly Bear Study Team).

During 1977–96, field crews visited and sampled sites where radio-marked grizzly bears had been located by aerial telemetry. Feeding activity was not documented at many of these bear-specific locations, although bear signs were found at most sites (Mattson, 1997a). Field crews identified and analyzed additional grizzly bear activity sites while on the way to and from radio-telemetry locations selected for sampling. Feeding activity at these sites was not ascribed to a specific bear. Our subsampling of bear telemetry locations for visitation was representative and not random, primarily because of logistical constraints imposed by limited funding and limited helicopter access to the Yellowstone ecosystem area, which is mostly nonroaded (Mattson, 1997a). Approximately 88% of the primary study area was >500 m from a road of any type.

We classified all grizzly bear activity sites according to the habitat type and cover type used to map grizzly bear habitat in the Yellowstone ecosystem (Mueggler and Stewart, 1980; Steele and others, 1983; Mattson and Despain, 1985). Field crews also described the targeted food and the intensity of associated feeding. During 1986–96, the extent or intensity of feeding activity was quantified (Mattson, 1991; Mattson, 1997a). For example, the volume of log, hill, or red squirrel midden debris excavated by bears foraging for ants or whitebark pine seeds was estimated (Mattson, 2001). Excavated whitebark pine cones were also counted (Mattson and Reinhart, 1997). The number of excavations for root foods and the number of roots obtained per individual excavation were estimated, as was the total volume of earth excavated in pursuit of rodents and the total number of rodent root caches or nests exploited (Mattson, 2004). Feces present at a feedsite were counted. Thus, for each activity site where feeding activity was found, grizzly bear activity was characterized by total volumes of excavations, as well as by total numbers of excavations, rodent nests, cones, and/or feces, in terms that could be compared among sites for a given feeding activity.

During 1986–96, field crews collected other data that pertained to the nutrient content of foods and the energetic costs of food extraction. A claw-o-meter (Holcroft and Herrero, 1984; Mattson, 1997c) was used to estimate how easy or difficult it was to excavate various substrates, including soils, logs, and anthill and squirrel midden debris. These measures provided a representation of energy expenditure (in maximum kilograms of resistance) that was comparable among sites and feeding activities. Samples of bear foods were also collected at feeding sites and analyzed for nutrient content (crude protein, crude fiber, total dietary fiber, starch, and ash). Other authors analyzed the nutrient content of foods for which we did not collect this information (e.g., whitebark pine seeds and army cutworm moths [Mattson and Reinhart, 1994; White, 1996]). In addition, we obtained seasonal estimates of ungulate carcass composition from Mitchell and others (1976), Anderson (1981), Bubenik (1982), Swift (1983), and Berger and Peacock (1988). Pond and Ramsay (1992) provided general allometric relations between adipose reserves and body mass. In combination with the work of Pritchard and Robbins (1990), these data allowed us to estimate amounts of digested energy and nutrients, comparable among foods and seasons.

We obtained estimates of volumes consumed per bite or other measured indicators of feeding activity at grizzly bear feedsites or derived this information from published research. Numbers of seeds were counted in whitebark pine cones. Bite sizes of foliage (in grams, dry weight per bite) were estimated by simulating grizzly bear grazing (Hudson and Frank, 1987) and were confirmed by comparison with published observations of grizzly bear bite sizes estimated under controlled conditions (Gross and others, 1993a, 1993b). Bite sizes of roots were estimated by weighing samples of excavated representative plants (Mattson, 1997c). Bite sizes of berries were derived from Welch and others (1997), assuming 1.5 berries per bite. Sizes of rodent root caches were estimated from excavated samples (Mattson, 2004) and were confirmed by comparison with estimates in Stuebe and Anderson (1985). Total mass consumed from ungulates was based on the species, gender, and age class, estimated amount of total edible biomass consumed by bears, and standardized tables of edible biomass for different carcass types (Mattson, 1997b). We obtained point estimates of ant, hornet, worm, and rodent biomass consumed per nest or unit volume of excavated material from the published literature (ants and hornets: Brian, 1978; Peakin and Josen, 1978; Akre and others, 1980; Redford and Dorea, 1984; Noyce and others, 1997; worms: Lawrence and Millar, 1945; Grant, 1955; Lee, 1985; rodents: Hansen and Bear, 1964; Pitts and Bullard, 1968; Hansen and Reid, 1973; Pinter, 1979; Anderson and MacMahon, 1981; Chase and others, 1982; Campbell and Dobson, 1992).

Field crews also collected bear feces while sampling grizzly bear activity sites from 1977 to 1996. During 1989–96, we also recorded the total volume of each collected feces. We used this information in conjunction with scat correction factors (milliliter of fecal volume to milligram of ingested mass; Hewitt and Robbins, 1996) and estimates of proportional fecal composition (Mattson and others, 1991a) to estimate ingested diet on a seasonal basis for 1989, 1991, and 1992, excluding feces that were known or suspected to be from black bears. Our analysis used these estimates of ingested diet for these 3 years. We did not estimate seasonal ingested diet for 1990 because some raw data were not available.

Analysis Methods

Our analysis methods were defined by three major tasks. First, we estimated relative net energy digested per gram of ingested food, by season where a difference was evident. Second, we estimated relative net gain of energy per feeding site by season and habitat type. Third, we estimated relative density of bear feeding activity by season, region, and habitat type, controlling for the effects of proximity to roads and other major human-related physical features (developments). We calculated final coefficients as the product of relative density of feeding activity times average relative net energy digested per feeding site (feedsite). The following sections describe the strata and methods that we used for each task. Table 1 lists and defines the variables that we used in calculations.

Stratifications

We calculated coefficients for several spatial and temporal stratifications. Spatial stratifications were by (1) habitat type, (2) ungulate winter range, (3) ecosystem region, and (4) forest and nonforest ecotone. Temporal stratifications were by (1) season and by type of year based on whether (2) whitebark pine seeds and/or ungulate carrion were heavily used or not. The following sections describe these stratifications in detail.

Spatial

Habitat Type

We stratified the study area into 18 forest/nonforest habitat types that were derived from previously mapped and identified mapping units (see Appendix 3 for a list of habitat types). Mapping units were described in previously published

Table 1. Description of variables used in calculation of coefficients of productivity ($coef_{jklmn}$) for grizzly bears, for habitat types in the Yellowstone ecosystem.

Variable	Description	Stratification
$avefs_{jklm}$	Average net digested energy per habitat type k	by season j, year type l, and region m; does not differ by edge type
$cfctr_{ij}$	Factor for converting units of feeding activity to grams ingested for each food i, averaged over years h	by season j; does not differ by habitat type, year type, region, or edge type
den_{jklmn}	Total density of bear activity in habitat type k	by season j, year type l, region m, and edge type n
ee_{ij}	Relative energy expended per gram of food i	by season j; does not differ by habitat type, region, year type, or edge type
fd_{jklmn}	Total density of feedsites in habitat type k	by season j, year type l, region m, and edge type n
$fslv_{ijk}$	Total units of feeding activity involving food i per feedsite in habitat type k	by season j; does not differ by region, year type, or edge type
$\sum fslv_{hij}$	Total units of feeding activity involving food i summed over all habitat types for year h	does not differ by region, year type, or edge type
$fsne_{ijk}$	Net digested energy from food i per feedsite in habitat type k	by season j; does not differ by region, year type, or edge type
$fvol_{hij}$	Total ingested grams of food i during year h (from fecal analysis)	does not differ by region, year type, or edge type
$iexc_{ij}$	Mean volume (cubic decimeter) excavated per individual excavation for food i	by season j; does not differ by habitat type, region, year type, or edge type
$imass_{ij}$	Mean grams of food i ingested per feedsite	by season j; does not differ by habitat type, region, year type, or edge type
$nete_{ij}$	Relative net digested energy per gram of food i	by season j; does not differ by habitat type, region, year type, or edge type
$pact_{jkl}$	Proportion of total activity in habitat type k that involved feeding of some type	by season j and year type l; does not differ by region or edge type
pde_{ij}	Percent of total energy digested from food i	by season j; does not differ by habitat type, region, year type, or edge type
$prop_{ijklm}$	Proportion of total feeding activity in habitat type k involving food i	by season j, region m, and year type l; does not differ by edge type
$resist_{ij}$	Kilogram of resistance per individual excavation for food i	by season j; does not differ by habitat type, year type, region, or edge type
te_{ij}	Total energy content per gram of food i	by season j; does not differ by habitat type, year type, region, or edge type
$vexc_{ij}$	Mean total volume (cubic decimeter) excavated per feedsite involving food i	by season j; does not differ by habitat type, year type, region, or edge type

cover type and habitat type classifications (see Pfister and others, 1977; Mueggler and Stewart, 1980; Steele and others, 1983; Mattson and Despain, 1985). Habitat type maps were based on interpreting aerial photographs and field-classifying the delineated polygons (Mattson and Despain, 1985). We updated these maps to account for the effects of extensive fires that occurred during 1988 by analyzing satellite imagery. We used prefire and postfire maps in analyses, depending on the date that data were collected. We defined the 18 habitat types used in this study by clustering the previously mapped habitat types described in Appendix 3 on the basis of similarities of grizzly bear activities within each (tables 2 and 3). We used Euclidean distances and average linkages for the initial statistical clustering. We made subjective refinements to this clustering based on site and vegetation similarities of habitat types (tables 2 and 3). In particular, we reassigned nonforest habitat types characterized by few ($n \leq 5$) samples of grizzly bear activity to the habitat categories of either mesic meadows and grasslands, wet meadows, or marshes and fens on the basis of site wetness and the related presence of indicative plant species (table 2). Small sample sizes caused unstable estimates of bear activity and made grouping of habitat types on the basis of other traits desirable for the purposes of mapping and description.

We lumped aggregate habitat types that were sparse (≤1% of the landscape) with other types that were more common based on similarities of site and vegetation features. Marshes and fens were uniformly rare and were combined with wet meadows for all analyses. High-water-table flux wetlands and clover patches were not mapped and were subsumed in areas identified as wet meadows. Miscellaneous other nonforest types (e.g., water and human features) were not included in the analyses.

Ungulate Winter Range

We stratified each region as being in bison winter range, in wapiti winter range, or in neither range. Bison winter range included areas used by wapiti and bison as well as areas used by bison alone. Wapiti winter range was not used by bison except incidentally. Ungulate winter ranges are a potentially important feature of grizzly bear habitat because grizzly bears in the Yellowstone ecosystem derive substantial energy from ungulates, principally from carrion on ungulate winter ranges (Mattson, 1997b). Furthermore, we distinguished between winter ranges with bison and those without because Yellowstone grizzly bears consume more meat from bison, per capita, than from any other ungulate species (Green and others, 1997; Mattson, 1997b).

For spring only (see the subsection on season, p. 10), we calculated a coefficient that applied to all habitat types within and outside of ungulate winter ranges if an effect of winter range was evident statistically (see subsection on year type by bear use of ungulate carrion, p. 12). We did not investigate interactions between winter range and habitat type because of insufficient sample sizes. We usually did not detect an effect of ungulate winter range where winter range was closely associated with specific habitat types. In these cases, habitat type, as such, functioned as a surrogate for the distribution of winter ranges.

Bull bison in central Yellowstone National Park. Bison are heavily scavenged by grizzly bears and provide the bears with more meat per carcass than any other type of scavenged ungulate (photo by Interagency Grizzly Bear Study Team).

Ecosystem Region

We calculated coefficients for each habitat type for each of four regions within the Yellowstone ecosystem that were identified with existing BMUs (figs. 1 and 2). We had identified these regions for previous analyses and found them to be associated with differences in abundance of key bear foods and grizzly bear foraging behavior (Mattson, 1997a, 1997b). Knight and others (1984) and Despain (1990) provide additional descriptions of these regions. We included the following BMUs in each of the four regions: in the north, Gallatin (#2), Washburn (#9), and Lamar (#5) BMUs; in the east, Crandall/Sunlight (#6) and Shoshone (#7) BMUs; in the west, Firehole/Hayden (#10) and Madison (#11) BMUs; and, in the south, Pelican/Clear (#8), Two Ocean/Lake (#14), Thorofare (#15), and Buffalo/Spread Creek (#17) BMUs. Some BMUs on the periphery of the Yellowstone ecosystem, known to be undersampled, were excluded from analysis (fig. 2; Hilgard [#1], Hellroaring/Bear [#3], Boulder/Slough [#4], Henry's Lake [#12], Plateau [#13], South Absaroka [#16], and Bechler/Teton [#18]). Coefficients calculated for regions containing BMUs #1, #3, #4, and #16 would apply in these areas. We have not yet determined appropriate sources of extrapolation for BMUs #12, #13, and #18.

We also stratified the south and west regions on the basis of BMUs that did and did not contain substantial numbers of bison year-round. Identification of BMUs with a "bison effect"

Table 2. Aggregate nonforest habitat types were defined by clustering constituent nonforest habitat types on the basis of grizzly bear activity in each type. Characteristic bear activities are shown as a percent of the total observations of bear activity within each type.

[Numeric designations are given for each type in parenthesis. Habitat types are further defined in Appendix 3. An asterisk (*) indicates a habitat type reallocated on the basis of similarity of site characteristics]

Aggregate and constituent nonforest habitat types (numeric designation)	Characteristic activities in habitat type (percent)	
Talus and scree (00007)	Digging moths	85%
	Bedding	15%
Lithic ridges (00004)	Digging biscuitroots	75%
Lithic alpine	No feeding sign	14%
Geum rossii/Trifolium parryi	Grazing clover	9%
Festuca idahoensis/Delphinium bicolor		
F. idahoensis/Arenaria congesta		
Lithic *F. idahoensis*		
Lithic *Artemisia tridentata*		
Lithic *Poa* spp.		
Lithic *Lomatium triternatum*		
Lithic forb		
Dry meadows and grasslands (00002)	No feeding sign	54%
Festuca idahoensis/Agropyron spicatum	Grazing graminoids	17%
F. idahoensis/Stipa richardsonii	Digging biscuitroots	15%
F. idahoensis/Agropyron caninum	Digging pocket gophers	14%
*F. idahoensis/Deschampsia caespitosa**	Digging yampa	9%
*Artemisia tridentata/F. idahoensis-F. idahoensis**		
Potentilla fruticosa/F. idahoensis		
Barren geothermal		
Mesic geothermal		
Mesic meadows and grasslands (00006)	Digging yampa	28%
F. idahoensis/Agropyron caninum-Geranium viscosissimum	Grazing graminoids	24%
Phleum alpinum/A. caninum-Carex microptera	Digging pocket gophers	22%
Artemisia tridentata/F. idahoensis-Geranium viscosissimum	Digging ants (anthills)	16%
Artemisia cana/F. idahoensis	No feeding sign	11%
Lupinus argenteus/Fragaria virginiana		
Clover patches (00001)	Grazing clover	100%
	Grazing graminoids	33%
	Flipping rocks	33%
Wet meadows (00008)	Grazing graminoids	41%
Salix geyeriana/Calamagrostis canadensis	No feeding sign	31%
S. geyeriana/Fragaria virginiana	Digging pocket gophers	12%
Salix wolfii/Carex aquatilis	Browsing elk thistle	9%
S. wolfii/Fragaria virginiana	Digging yampa	9%
Artemisia cana/Carex aquatilis	Bedding	9%
A. cana/Fragaria virginiana		
Potentilla fruticosa/Deschampsia caespitosa		
Carex aquatilis/Pedicularis groenlandica		
C. aquatilis/Deschampsia caespitosa		
Calamagrostis canadensis/Deschampsia caespitosa		
*C. canadensis/Senecio triangularis**		
Deschampsia caespitosa/Carex spp.*		
*D. caespitosa/Juncus balticus**		
Phleum alpinum/Carex aquatilis		
P. alpinum/C. microptera		
Heracleum lanatum/Rudbeckia occidentalis		
Marshes and fens (00005)	No feeding sign	47%
Salix geyeriana/Carex rostrata	Grazing graminoids	33%
Carex aquatilis/Salix phylicifolia	Ungulates	22%
Carex rostrata/C. rostrata		
Calamagrostis canadensis/C. canadensis		
Scirpus olneyi/S. olneyi		
High-water-table flux wetlands (00003)	Digging pondweed	100%
Carex vesicaria/C. vesicaria	Grazing graminoids	33%

Table 3. Aggregate forest habitat types were defined by clustering constituent forest habitat types on the basis of grizzly bear activity in each type. Characteristic bear activities are also shown as a percent of the total observations of bear activity within each type.

[Acronym and numeric designation are given for each type in parentheses. Habitat types are further defined in Appendix 3]

Aggregate and constituent forest habitat types (acronym and numeric designation)	Characteristic activities in habitat type (percent)	
Low elevation spruce-dominated sites (LPIEN, 10601)	No feeding sign	54%
Picea engelmannii/Equisetum arvense	Grazing graminoids	17%
P. engelmannii/Galium triflorum	Grazing horsetail	17%
	Digging ants (logs)	14%
	Ungulates	9%
Low elevation lodgepole pine-dominated sites (LPICO, 10501)	No feeding sign	49%
Abies lasiocarpa/Carex geyerii	Digging ants (logs)	20%
Pinus contorta/Purshia tridentata	Bedding	16%
P. contorta/Festuca idahoensis	Ungulates	14%
P. contorta/Calamagrostis rubescens		
P. contorta/Carex geyerii		
P. contorta/Carex rossii		
Mesic Douglas-fir-dominated sites (MPSME, 10801)	Digging ants (logs)	44%
Pseudotsuga menziesii/Symphoricarpos albus	No feeding sign	40%
P. menziesii/Calamagrostis rubescens	Bedding	9%
P. menziesii/Spiraea betulifolia		
Abies lasiocarpa/Vaccinium globulare-V. globulare		
Populus tremuloides series		
Mesic subalpine fir climax sites (MABLA, 10701)	No feeding sign	51%
Abies lasiocarpa/Actaea rubra	Digging ants (logs)	20%
A. lasiocarpa/Thalictrum occidentale	Bedding	14%
A. lasiocarpa/Symphoricarpos albus	Grazing	8%
A. lasiocarpa/Calamagrostis rubescens	Ungulates	7%
A. lasiocarpa/Calamagrostis canadensis	Digging sweet-cicely	6%
A. lasiocarpa/Osmorhiza chilensis		
High elevation or dry Douglas-fir-dominated sites (HPSME, 10301)	No feeding sign	71%
Pseudotsuga menziesii/Juniperus communis	Bedding	15%
P. menziesii/Arnica cordifolia	Digging ants (logs)	9%
P. menziesii/Symphoricarpos oreophilus	Grazing graminoids	9%
P. menziesii/Berberis repens		
Abies lasiocarpa/B. repens		
High elevation subalpine fir climax sites (HABLA, 10101)	No feeding sign	58%
Abies lasiocarpa/Vaccinium globulare-V. scoparium	Digging ants (logs)	17%
A. lasiocarpa/Juniperus communis	Bedding	11%
A. lasiocarpa/Arnica cordifolia	Whitebark pine seeds	11%
Pinus albicaulis/Vaccinium scoparium		
Sites dominated by grouse whortleberry (HVASC, 10401)	No feeding sign	63%
Abies lasiocarpa/Vaccinium scoparium-Calamagrostis rubescens	Digging ants (logs)	16%
A. lasiocarpa/Vaccinium scoparium-V. scoparium	Bedding	12%
Pinus contorta/Vaccinium scoparium	Whitebark pine seeds	9%
High elevation whitebark pine dominated sites (HPIAL, 10201)	Whitebark pine seeds	45%
Abies lasiocarpa/Arnica latifolia	No feeding sign	35%
A. lasiocarpa/Vaccinium scoparium-Pinus albicaulis	Digging ants (logs)	11%
Pinus albicaulis/Festuca idahoensis	Bedding	9%
Whitebark pine cover types on any habitat type		
Dry forest openings created by timber harvest of fire (10100)	No feeding sign	58%
Seedling-sapling cover type on LPICO, HVASC, HPSME, HABLA, and HPIAL	Grazing graminoids	16%
	Bedding	11%
	Digging ants	11%
Mesic forest openings created by timber harvest or fire (10600)	No feeding sign	44%
Seedling-sapling cover type on LPIEN, MPSME, and MABLA	Grazing graminoids	24%
	Bedding	11%
	Digging ants	10%

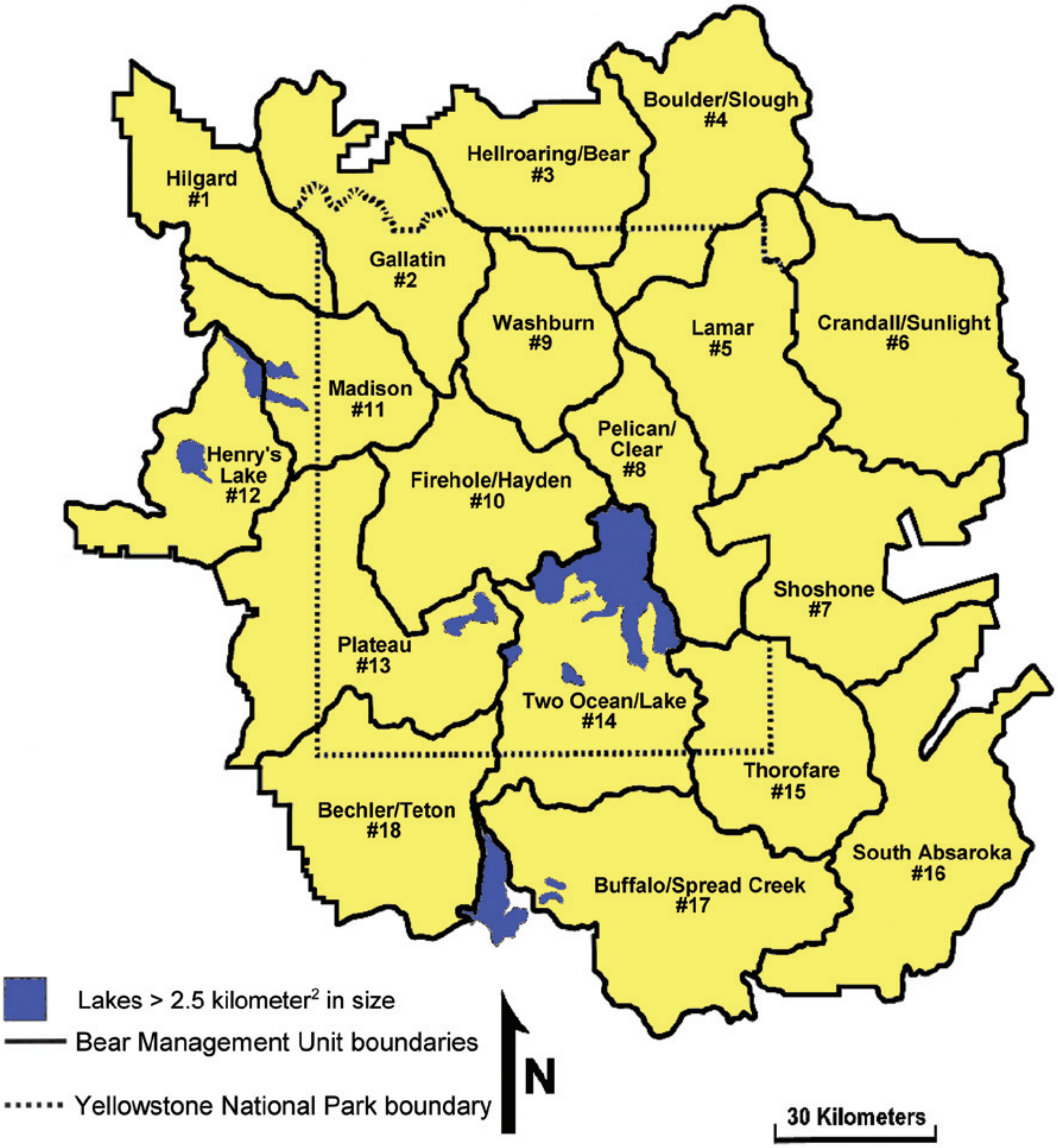

Figure 1. Map of the Yellowstone grizzly bear study area showing Yellowstone National Park (delineated by a dashed line) and the 18 numbered and named Bear Management Units that compose the Yellowstone grizzly bear recovery area.

was contingent on evidence that grizzly bears made substantial use of bison in these areas. In the south, the Pelican/Clear (#8) BMU and, in the west, the Firehole/Hayden (#10) and Madison (#11) BMUs were treated as containing year-round bison populations heavily used by bears; 84% of all grizzly bear use of bison during 1977–96 occurred in these three BMUs. We introduced this additional level of stratification because bison are so energetically important to bears (Mattson, 1997b) and because bison range in the Yellowstone ecosystem is highly circumscribed (Greater Yellowstone Coordinating Committee, 1987).

Forest/nonforest Ecotone

We further stratified habitat types by whether they were within or beyond 100 m of forest/nonforest edge; 100 m was roughly the extent of this ecotone's effect on grizzly bear foraging activity (Graham, 1978; Blanchard, 1983; Mattson, 1997c). We calculated coefficients for forest/nonforest edge by region and season but only in instances where an effect of edge was statistically evident. We did not investigate interactions between ecotone and habitat type because of insufficient sample sizes. We also did not estimate differences in the proportional occurrence of feeding activities by habitat type

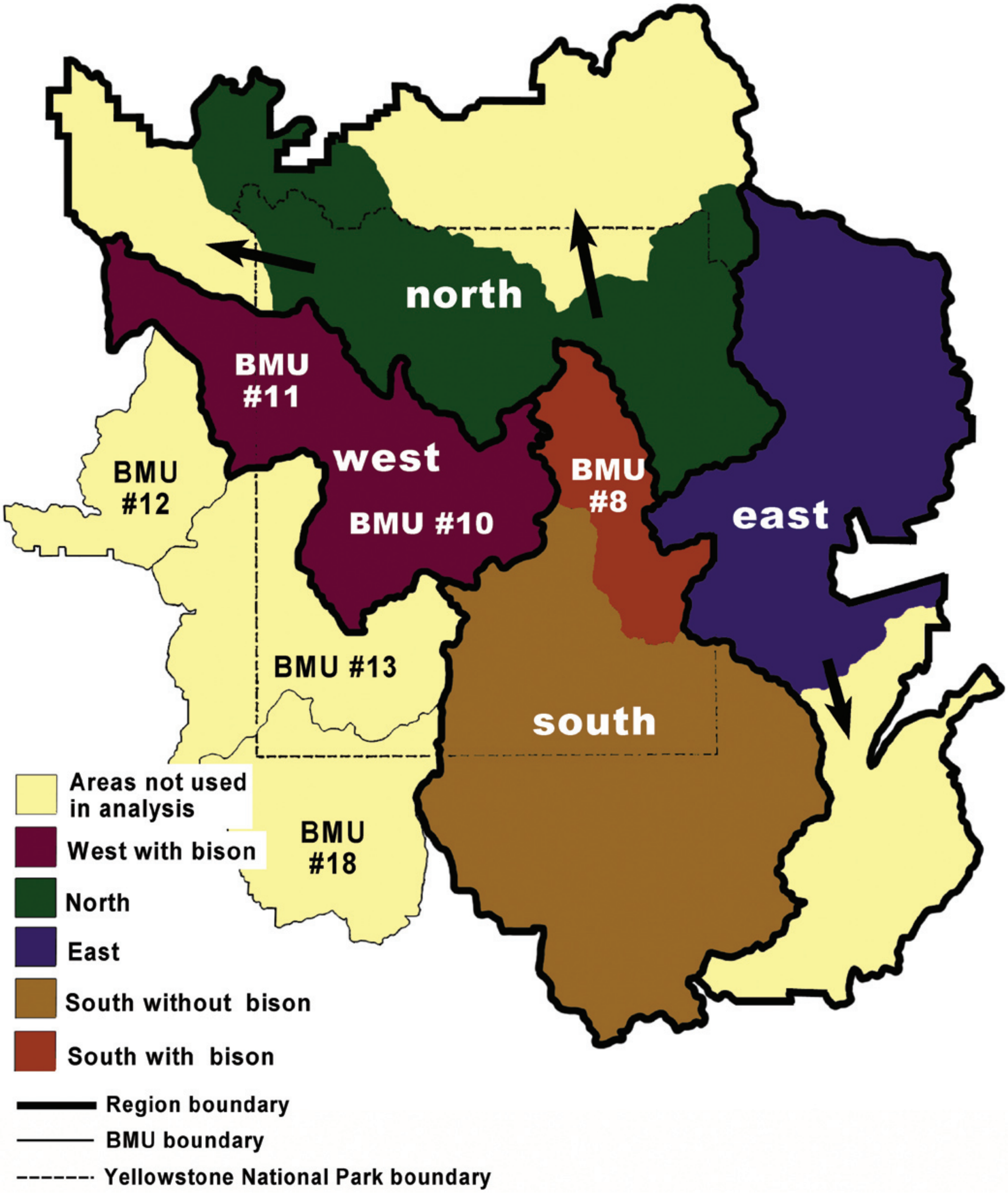

Figure 2. Map of the Yellowstone grizzly bear recovery area showing delineations of regions (north, east, south, and west). Bear Management Units (BMUs) from which data were used for development of cumulative effects model coefficients are colored green, purple, or brown. BMUs with year-round bison populations used heavily by grizzly bears are identified by number (BMUs #8, #10, and #11). The boundary of Yellowstone National Park is shown as a dashed line. Arrows indicate the source of coefficients applied to BMUs (colored yellow) that were not used in calculations.

for areas within and beyond ecotones, again because of limited sample sizes.

Temporal

Season

We calculated coefficients for each spatial stratification (habitat type, ungulate winter range, ecosystem region, and forest/nonforest ecotone) for each of four seasons of bear activity—spring, estrus, early hyperphagia, and late hyperphagia (table 4). Early hyperphagia was of shorter duration than the other seasons.

Year Type by Bear Use of Whitebark Pine Seeds

We calculated coefficients for each spatial stratification, for early and late hyperphagia only, distinguishing between years for which consumption of whitebark pine seeds by grizzly bears was a major feeding activity and years for which it was not. We based determinations of year type on the level of use of pine seeds by bears, which was evident in feces collected at feedsites and examined during field sampling of grizzly bear radio-telemetry locations (tables 5–7). Heavy use roughly corresponded to years when mean cone production on whitebark pine trees at permanent transects exceeded 20 cones per tree, compared to years when production was <20 cones per tree (Mattson and Reinhart, 1994).

Whitebark pine tree on Mount Washburn in Yellowstone National Park. The whitebark pine produces cones with large fat-rich seeds that are a major food of especially female grizzly bears (photo by David Mattson, U.S. Geological Survey).

Table 4. Definition of seasons for analyzing Yellowstone grizzly bear data.

Season	Definition
Spring—*den emergence through 15 May*	Approximately corresponds to hypophagia (sensu Nelson and others, 1983) and the period during which ungulate carrion is available to and used by grizzly bears on ungulate winter ranges (Mattson, 1997b; Green and others, 1997).
Estrus—*16 May through 15 July*	Approximately corresponds to the mating season and the period of female estrus (Schleyer, 1983; Craighead and others, 1995); this period also begins with the advent of predation on wapiti calves (Gunther and Renkin, 1990) and coincides with the period during which the majority of fishing for spawning cutthroat trout occurs (Reinhart and Mattson, 1990; Mattson and Reinhart, 1995).
Early hyperphagia—*16 July through 30 August*	Approximately corresponds to the early part of hyperphagia (sensu Nelson and others, 1983), as indicated by an escalation in feeding activity (Mattson and others, 1991a; Mattson, 1997a). This period is distinguished by the unavailability of whitebark pine seeds from the current year's crop (Mattson and others, 1994), by the advent of foraging in alpine cirques for army cutworm moths (Mattson and others, 1991b; French and others, 1994), and by an increase in excavations for roots of biscuitroot and yampa (Mattson and others, 1991a).
Late hyperphagia—*1 September through advent of denning*	Approximately corresponds to the later part of hyperphagia (sensu Nelson and others, 1983), as indicated by continued high levels of feeding activity (Mattson and others, 1991a; Mattson, 1997a). This period is distinguished by the excavation of red squirrel middens for whitebark pine seeds from the current year's crop, during years when seed crops are relatively large (Mattson and others, 1994). This period also corresponds to an escalation in consumption of ungulates related to rutting activity and post-rut mortality of bull bison, wapiti, and moose (Mattson, 1997b), and the availability of carcass remains from ungulates killed by hunters.

Table 5. Frequency of feeding activity and percent volume in feces related to grizzly bear use of ungulates in the spring and whitebark pine seeds during estrus and hyperphagia in the Yellowstone ecosystem, 1973-96. Counts of carcasses from transects in the Firehole/Hayden winter range and of cones from whitebark pine transects are also given.

[Numbers in bold meet criteria for a "use" year (Y) either for ungulates or whitebark pine seeds, while numbers in parentheses are based on small (≤20) samples]

Year	Spring ungulate use					Early season (estrus early hyperphagia) Whitebark pine seed use				Late hyperphagia Whitebark pine seed use				
	Ungulate feedsites		Volume in May feces		Carcass counts	Pine seed feedsites		Volume in feces		Pine seed feedsites		Volume in September feces		Cone counts
	Percent	*n*	Percent	*n*	*n*	Percent	*n*	Percent	*n*	Percent	*n*	Percent	*n*	*n*
73												**(32)**[eh]	**(25)**[eh]	
74												(8)[eh]	(99)[eh]	
75										(4%,	n = 68)[f]	(5%,	n = 37)[g]	
76										**(45%,**	**n = 23)**[f]	**(73%,**	**n = 29)**[g]	
77	4	76	38	37		0	44	2	212	(0)	13	0	27	
78	24	55	(29)	11		2	174	3	364	**(33)**	12	**60**	**92**	
79	13	47	11	61		**12**	**162**	**51**	**579**	**51**	**82**	**74**	**111**	
80	35	40	(37)	20		2	45	8	240	**51**	**39**	**(25)**	12	**26**
81	9	23	3	26		6	51	5	161	(0)	6	(0)	5	13
82	(Heavy winter kill)					(40)	20	6	99	8	24	2	39	17
83	(80)[a]	15	(15)	15		(0)	17	1	190	(0)	1	(0)	6	17
84	--	0	(18)	11		(0)	1	2	343	--	0	(50)	8	6
85	4	53	(5)	20	51	(0)	7	10	355	**27**	**26**	**72**	**43**	**27**
86	(17)	12	17	32	74	**17**	**209**	**18**	**324**	2	82	9	109	1
87	11	56	2	42	16	**14**	**280**	**23**	**292**	**40**	**104**	**64**	**78**	2
88	16	74	18	27	47	2	323	1	215	0	79	0	61	2
89	**52**	**56**	**33**	**85**	**325**	5	288	5	366	**75**	**61**	**62**	**133**	**49**
90	2	53	5	33	6	**10**	**264**	**25**	**401**	15	40	13	74	2
91	(0)	11	**24**	**44**		2	235	4	248	**58**	**64**	**77**	**70**	16
92	13	90	6	31	(32)[c]	1	189	2	153	**48**	**54**	**53**	**41**	15
93	**27**	**22**	**(18)**[b]	**(59)**[b]	(21)[c]	0	99	(0)[d]	(150)[d]	(0)	20	(15)[h]	(33)[h]	10
94	(0)	14	(9)[b]	(64)[b]	(6)[c]	0	99	(0)[d]	(119)[d]	0	33	(2)[h]	(32)[h]	2
95	(12)	17	(6)[b]	(50)[b]	(24)[c]	1	83	(0)[d]	(54)[d]	(0)	4	(0)[h]	(7)[h]	3
96	(20)	4	(2)[b]	(20)[b]	(35)[c]	7	60	(12)[d]	(39)[d]	**86**	**29**	**(75)**[h]	**(47)**[h]	**25**

[a] During 1983 crews oversampled sites where bears fed on ungulates.

[b] These values were obtained from IGBST annual reports and are for the period March-June. Raw data for these years were not available for analysis.

[c] These counts were obtained using a different protocol compared to 1985-90.

[d] These values were obtained from IGBST annual reports and are for the period July-August. Raw data for these years were not available for analysis.

[e] These values were obtained from summaries in Mealey (1975). Raw data for these years are unavailable.

[f] These values were obtained from the 1976 IGBST annual report and are for the entire year. Raw data for these years are unavailable.

[g] These values were obtained from summaries in Blanchard (1978) and are for the entire year. Raw data for these years are unavailable.

[h] These values were obtained either from IGBST annual reports or Mealey (1975) and are for the period September-October. Raw data were unavailable for analysis.

Table 6. Rule set for classifying years as either being a heavy (Y = yes) or light (N = no [not heavy]) year for Yellowstone grizzly bear use of ungulate carrion and whitebark pine seeds.

[Determinations for each year are given in table 7]

Spring use of ungulate carrion[1]

If either percent ungulate feedsites ≥ 20 (and $n > 20$) or percent ungulate volume in May feces ≥ 20 (and $n > 20$), then UNG[2] = Y.

If $n \leq 20$ for feedsites and feces then UNG = Y if percent ungulate feedsites ≥ 20 and percent ungulate volume in May feces ≥ 20.

Late hyperphagia use of whitebark pine seeds[3]

If either percent whitebark pine feedsites ≥ 20 (and $n > 20$) or percent whitebark pine seed volume in September feces ≥ 20 (and $n > 20$), then WBP(L)[4] = Y.

If $n \leq 20$ for feedsites and feces then WBP(L) = Y if percent whitebark pine feedsites ≥ 20 and percent whitebark pine seed volume in September feces ≥ 20.

If information on feedsites and feces is missing, then WBP(L) = Y if mean cone count/tree ≥ 20.

Early season (estrus – early hyperphagia) use of whitebark pine seeds

If either % whitebark pine feedsites ≥ 10 (and $n > 20$) or percent whitebark pine seed volume in feces ≥ 15 (and $n > 20$), then WBP(E)[5] = Y.

If $n \leq 20$ for feedsites and feces then WBP(E) = Y if percent whitebark pine feedsites ≥ 10 and percent whitebark pine seed volume in feces ≥ 15.

Year-long use of whitebark pine seeds

If either WBP(E) or WBP(L) = Y then WBP(year-long) = Y.

---

[1] May feces were used for determining spring levels of ungulate use because of the greater sample sizes collected during this month and because fecal volumes at this time are more sensitive to the abundance of carrion, given the greater number of foraging options available.

[2] "UNG" is the variable name used in our calculations to denote whether grizzly bears made heavy (Y) or light (N) use of ungulates during spring of that year.

[3] September feces were used for determining levels of whitebark pine seed use during late hyperphagia because of the relatively consistent sample sizes collected during this month, in contrast to the considerable variation in sample sizes or absence of data collected during October.

[4] "WBP(L)" is the variable name used in our calculations to denote whether grizzly bears made heavy (Y) or light (N) use of whitebark pine seeds during late hyperphagia of that year.

[5] "WBP(E)" is the variable name used in our calculations to denote whether grizzly bears made heavy (Y) or light (N) use of whitebark pine seeds during early hyperphagia of that year.

Year Type by Bear Use of Ungulate Carrion

We calculated coefficients for each spatial stratification, for spring only, distinguishing between years for which consumption of carrion by grizzly bears was a major feeding activity and years for which it was not. We based determinations of year type on the level of ungulate use by bears evident in feces collected and at feedsites examined during field sampling of grizzly bear radio-telemetry locations (tables 5–7). Heavy use of carrion roughly corresponded to years when the number of carcasses found on ungulate carcass transects exceeded 40 carcasses compared to years when this count was lower (Green and others, 1997).

Net Energy Digested per Gram of Ingested Food

We calculated a relative measure of the net energy digested per gram of dry weight ingested food ($nete_{ij}$) for feeding activity i and season j as the product of total energy (te_{ij}) times percent energy digested (pde_{ij}) minus an index of energy expended (ee_{ij}): $nete_{ij} = [(te_{ij} \times pde_{ij}) - ee_{ij}] + 0.1$. We calculated seasonal values only where a seasonal effect was evident ($\alpha = 0.1$) by analysis-of-variance for some parameter included in the calculation. All values were log-transformed for these tests to meet the assumptions of normality and homogeneity of variance. This measure only accounted for expenditures immediately associated with extracting the food from its enclosing matrix or shearing it from supporting tissue and did not account for costs of search and movement, either within or between sites.

Total energy content. — We calculated total energy content (te_{ij}, in kilocalories) as a function of the energy contained in each nutrient and the dry weight nutrient composition of the ingested fraction of the food. This calculation excluded, for example, skeleton and viscera of ungulates (Green and others, 1997; Mattson, 1997b) and structural parts of whitebark pine cones (Mattson and Jonkel, 1990; Mattson and Reinhart, 1994). The calculation was: te_{ij} = (crude protein × 4.3) + (ether extract × 9.4) + (starch × 4.2) + (sugar × 3.8) + (ash × 0) + (remainder [carbohydrate] × 4.2), where each nutrient was expressed as a proportion of total dry weight (fig. 3). Remaining carbohydrate was calculated by subtraction. We obtained energy contents from Robbins (1983) and Schmidt-Nielson (1990). We took nutrient contents of some foods from published research, most notably sugar and ether extract from Craighead and others (1982).

Percent digested energy. — We obtained estimates of percent digested energy (pde_{ij}) directly from Pritchard and

Table 7. Classification of years according to whether grizzly bear use of ungulate carrion was heavy during the spring (Y) or not (N), whether use of whitebark pine seeds was heavy during some time of the year (Y) or not (N), and whether whitebark pine seed use was heavy during late hyperphagia (Y) or not (N) in the Yellowstone ecosystem during 1973–96.

[Determinations were made based on information presented in tables 5 and 6]

Year	Classification by ungulate use (spring)	Classification by whitebark pine seed use (year-long)	Classification by whitebark pine seed use (late hyperphagia)
73		**Y**	**Y**
74		N	N
75		N	N
76		**Y**	**Y**
77	**Y**	N	N
78	**Y**	**Y**	**Y**
79	N	**Y**	**Y**
80	**Y**	**Y**	**Y**
81	N	N	N
82	**Y**	N	N
83	no data	N	N
84	N	N	N
85	N	**Y**	**Y**
86	N	Y	N
87	N	**Y**	**Y**
88	N	N	N
89	**Y**	**Y**	**Y**
90	N	Y	N
91	**Y**	**Y**	**Y**
92	N	**Y**	**Y**
93	**Y**	N	N
94	N	N	N
95	N	N	N
96	N	**Y**	**Y**

Robbins (1990) or from relationships that they presented. Unmodified values were used for ungulate meat (mule deer), cutthroat trout, rodents (ground squirrels), and whitebark pine seeds (pinyon pine). We estimated other digestibilities from their relationship to total dietary fiber (*tdf*): $pde_{ij} = 101.3 - (1.39 \times tdf)$. We obtained an estimate of digestibility for army cutworm moths from O'Brien and Lindzey (1994), who also referenced Pritchard and Robbins (1990). Total digested energy (den_{ij}) was the product of pde_{ij} times te_{ij}.

We related *tdf* to crude fiber (*cf*), ash (*ash*), and starch (*strch*) based on paired analyses of nutrients from a single sample, as follows:

$tdf = 6.63 + (1.54 \times cf) + (3.84 \times \ln ash)$; $R^2 = 0.88$, $F = 192.2$, df = 2, 51

$tdf = 15.1 + (1.56 \times cf)$; $r^2 = 0.87$, $F = 341.6$, df = 1, 52

$tdf = e^{(3.85\ \ [0.024 \times strch])}$; $r^2 = 0.50$, $F = 22.1$, df = 1, 22.

Because most analyses of nutrient content in this study did not include *tdf*, we based estimates of digestibility on these subsidiary relationships between *tdf* and *cf* or *tdf* and *strch*. We did not commonly analyze total dietary fiber because the use of *tdf* for estimating digestibility was not established until late in our study. We used simple relationships between *tdf* and *cf* or *tdf* and *strch* in a few cases because *cf* and *ash* were not analyzed for all samples. We did not analyze the joint effects of *strch* and *cf* because of high multicollinearity, which potentially resulted in unstable coefficients.

Relative energy expenditure. — We prorated relative energy expenditure to grams ingested and scaled the final calculation to derive as meaningful an index of net energy gain as possible (fig. 4). We obtained estimates of grams ingested ($imass_{ij}$) per feedsite from field samples and previously published research. We divided this value by volume (in cubic decimeters) of excavated material ($vexc_{ij}$) to obtain grams ingested per cubic decimeter of excavated material. We similarly divided kilograms of resistance ($resist_{ij}$) by mean volume of individual digs ($iexc_{ij}$) to obtain kilograms of resistance per cubic decimeter excavated. We then calculated kilograms of resistance per gram of food by dividing grams per cubic decimeter of excavated material into kilograms of resistance per cubic decimeter. We scaled this value assuming that grizzly bears obtained some net energetic reward from all feeding activities. The excavation of ants from logs provided the least energetic gain (digested kilocalories per gram) per unit of energy expended (kilograms of resistance per gram). We multiplied relative energy expenditure by a factor (*sfactor*) that produced a result equal to digested energy for excavation of ants from logs. We then multiplied energy expenditure for all other feeding activities by *sfactor*, which was the same for all foods and seasons, so as to standardize relative energy expenditure across all activity types. The calculation of ee_{ij} reduced to:

$$ee_{ij} = [(resist_{ij} \times vexc_{ij}) / (imass_{ij} \times iexc_{ij})] \times sfactor.$$

Prior to standardization (i.e., while still working in units of kilograms of resistance), we used expert judgement to assign relative energy expenditures to some activities, such as grazing and use of carcasses, that could not be simulated using the claw-o-meter. We ascribed costs to these activities by comparing visual observations of bears engaged in activities for which we had estimated energetic expenditure using the claw-o-meter with visual observations of bears engaged in activities for which we did not have direct estimates. On this basis, we ascribed a greater cost to use of bison and moose carrion compared to use of wapiti carrion because of differences in resistance of hide, viscera, and skeleton (Green and others, 1997). We also ascribed a greater cost to use of ungulates during early and late hyperphagia compared to use of ungulates during spring because predation was more frequent during the later seasons (Mattson, 1997b).

Final values of relative net digested energy ($nete_{ij}$) included the addition of 0.1 (see the first paragraph under

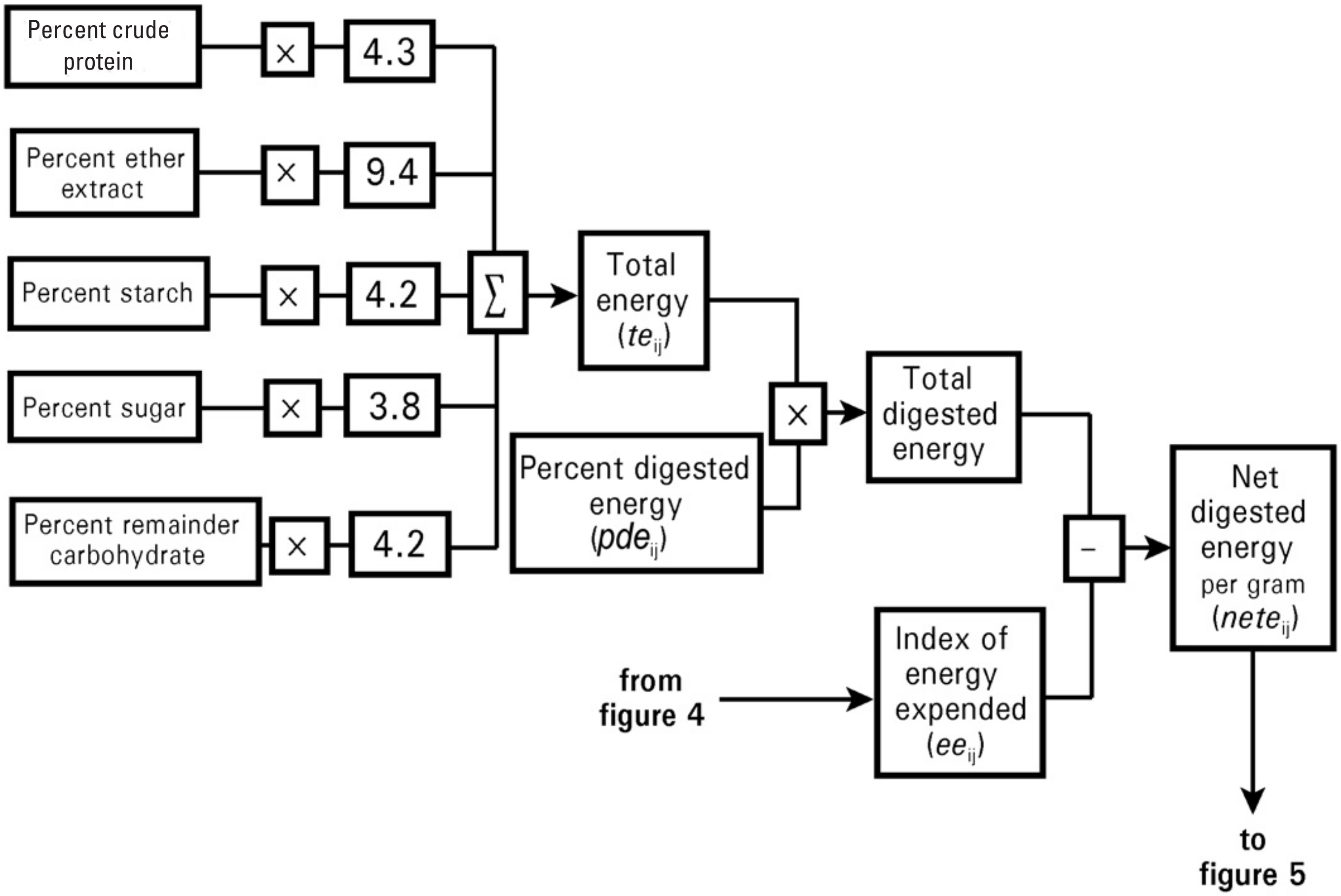

Figure 3. Schematic for the calculation of per gram net digested energy ($nete_{ij}$) for food i during season j, for foods used by grizzly bears in the Yellowstone ecosystem.

subsection "Net Energy Digested per Gram of Ingested Food," p. 12). We made this adjustment so that the excavation of ants from logs would contribute some value to the estimated aggregate productivity of habitat types. Without this addition, the excavation of ants from logs would have made no contribution and would have been assumed to be of no energetic benefit to bears. Because grizzly bears so commonly excavated logs, we judged this assumption to be untenable (see Noyce and others, 1997; Mattson, 2001).

Net Energy Digested per Feeding Site

We calculated a relative measure of net energy digested per feeding site ($fsne_{ijk}$) as the product of per gram net digested energy ($nete_{ij}$) times a conversion factor ($cfctr_{ij}$) that related grams ingested to units of feeding activity, times the mean level of feeding activity at a feeding site ($fslv_{ijk}$) in units unique to each activity: $fsne_{ijk} = nete_{ij} \times cfctr_{ij} \times fslv_{ijk}$ (fig. 5). Variation in $fsne_{ijk}$ among habitat types was due only to variation in mean level of feeding activity ($fslv_{ijk}$); per gram net digested energy and conversion factors did not differ among habitat types. We estimated net digested energy for each food i, specific to each season j, only where some season effect was evident (see first paragraph under subsection "Net Energy Digested per Gram of Food," p. 12). Where possible, we estimated conversion factors for each food and season. We estimated mean per feedsite level of feeding activity for all combinations of food, season, and habitat type k.

We estimated level of feeding activity ($fslv_{ijk}$) by the various measures of feeding intensity described under the section on "Field Methods," including, for example, total number of excavations, total volume of excavations, total kilograms of ingested meat, and total number of feces (+1, so that sites with no feces would receive some value). These measures were comparable among seasons and habitat types for a given feeding activity but were not comparable among activity types. In other words, total volumetric consumption of a given food associated with a given feeding activity would be apportioned among habitat types proportional to the intensity of that feeding activity. However, because units of measure for intensity differed among activity types it was not self-evident how, for example, number of root excavations compared to number of feces counted at a grazing site.

We used conversion factors ($cfctr_{ij}$) to translate the various units of measure for feeding intensity into common units

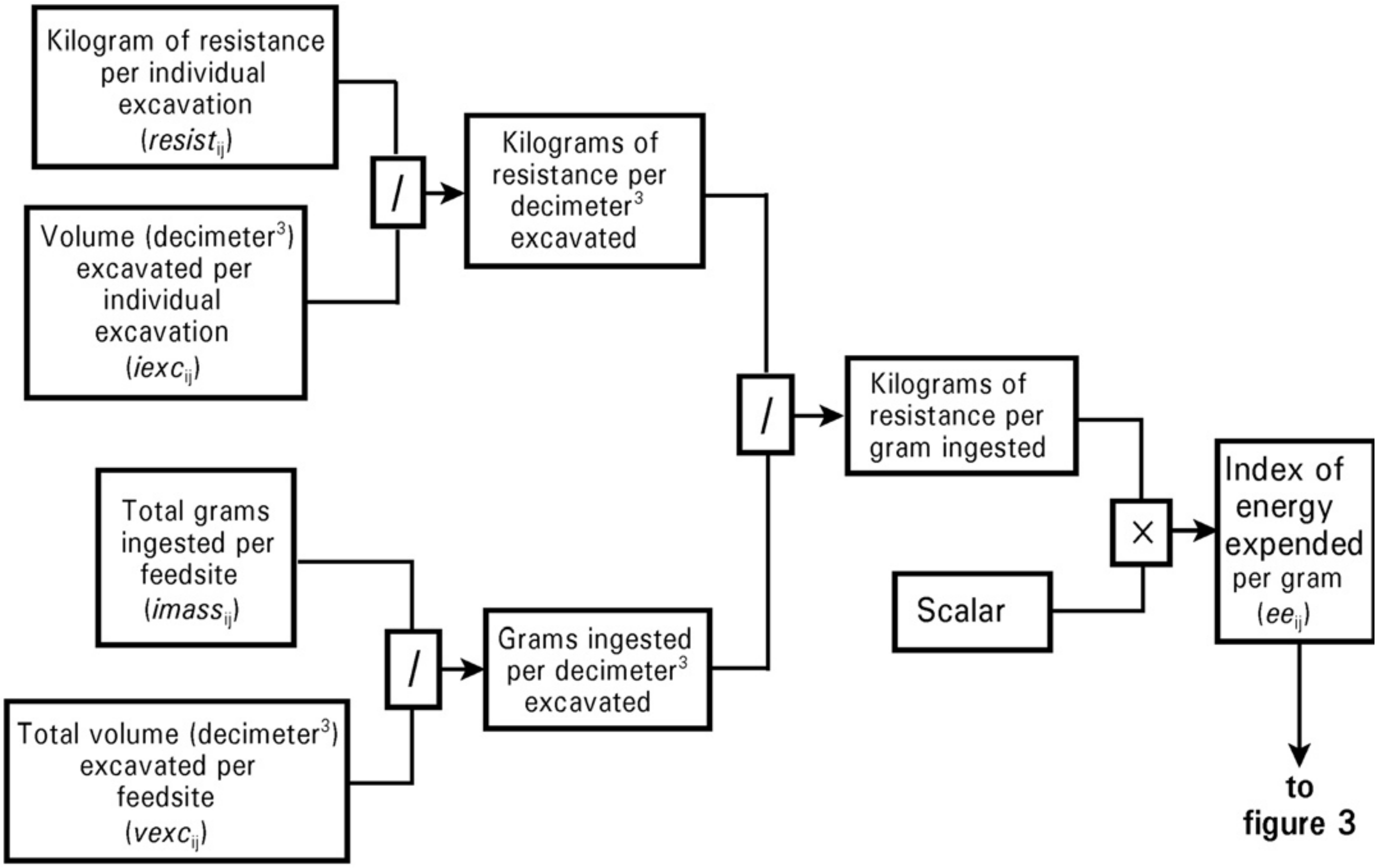

Figure 4. Schematic for calculation of the index of energy expended per gram (ee_{ij}) of food i ingested during season j, for foods used by grizzly bears in the Yellowstone ecosystem.

of grams ingested. We estimated conversion factors by dividing the total mass (in grams) of different foods ingested during a given year h (1989, 1991, or 1992; see "Field methods") and season j ($fvol_{\mathrm{hij}}$) by the summations of feeding activity units for the corresponding feeding activity and time period ($\Sigma\, fslv_{\mathrm{hij}}$): $cfctr_{\mathrm{hij}} = fvol_{\mathrm{hij}} / \Sigma\, fslv_{\mathrm{hij}}$. We used a mean among years, by season ($cfctr_{\mathrm{ij}}$), in final calculations. We estimated total ingested mass from contents of feces, converting milliliters of fecal volume to grams of ingested mass by factors given in Hewitt and Robbins (1996). We did not calculate conversion factors by habitat type because it was difficult to ascribe the contents of specific feces to specific sites and because of insufficient sample sizes.

Average Net Energy Digested per Feedsite by Habitat Type

We calculated the relative net energy digested per feeding site within a given habitat type k for season j, year type l, and region m ($avefs_{\mathrm{jklm}}$) as the average of the net digested energy ($fsne_{\mathrm{ijk}}$) of all feeding activities occurring in that time and place, weighted by their proportional frequencies ($prop_{\mathrm{ijklm}}$): $avefs_{\mathrm{jklm}} = [\Sigma\, (prop_{\mathrm{ijklm}} \times fsne_{\mathrm{ijk}})]$ over all foods i (fig. 6). We attributed variation in $avefs_{\mathrm{jklm}}$ among year types and regions only to variation in proportions of feeding activities; net digested energy per feedsite of a given type did not differ among these strata. We used all activity sites, whether ascribed to radio-marked bears or not, to estimate proportional frequencies of feeding activities. This approach approximately doubled sample sizes and was deemed defensible given that the greatest discrepancy between results from radio-marked bears and other bears was in the occurrence of nonfeeding activity that did not leave sign. In calculations where the occurrence of nonfeeding activity was judged to be consequential (see "Density of Feeding Activity," below), only activity sites from radio-marked bears were used.

Density of Feeding Activity

We calculated density of feeding activity (fd_{jklmn}) as the product of total density of bear activity (den_{jklmn}) times the proportion of that activity ($pact_{\mathrm{jkl}}$) that was associated with feeding: $fd_{\mathrm{jklmn}} = den_{\mathrm{jklmn}} \times pact_{\mathrm{jkl}}$; for season j, habitat type

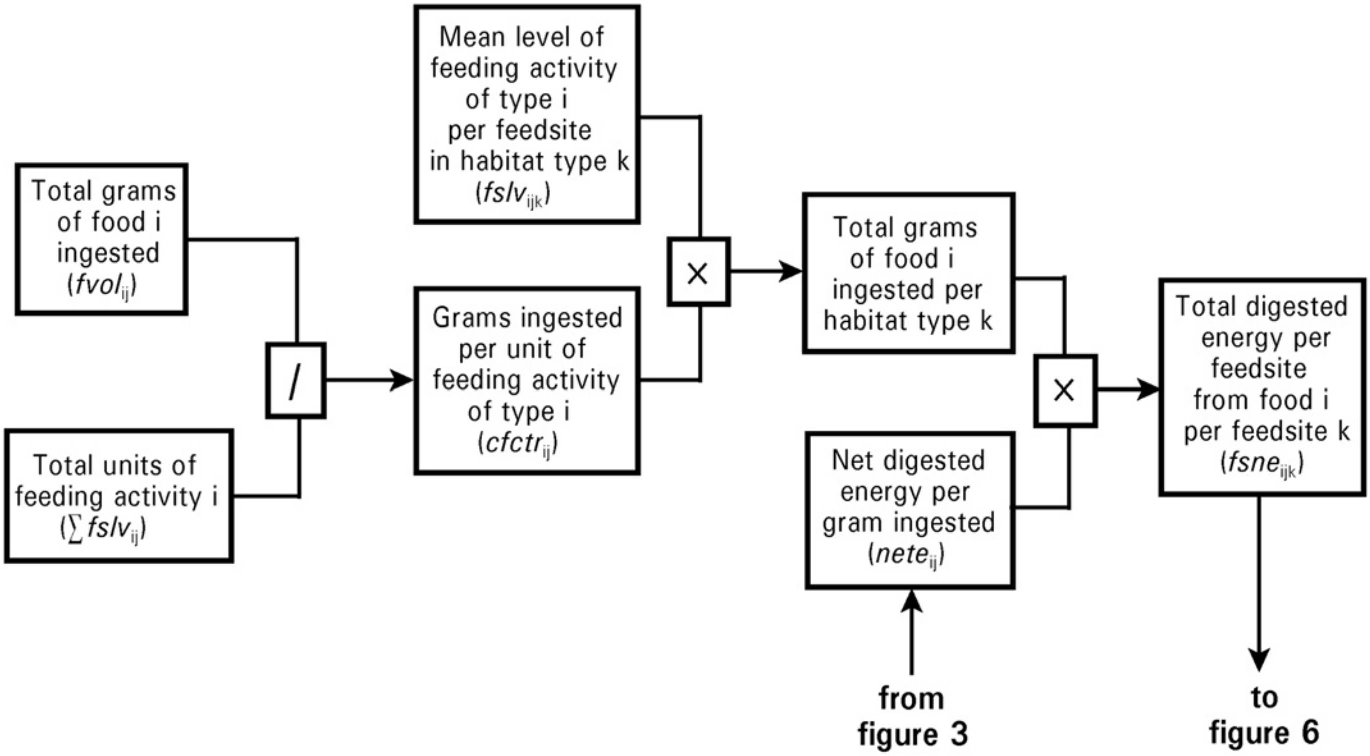

Figure 5. Schematic for the calculation of total digested energy per feedsite k from food i for season j ($fsne_{ijk}$), for foods and habitat types used by Yellowstone grizzly bears.

k, year type l, region m, and edge type n (fig. 6). Variation in fd_{jklmn} among regions and edge types was due only to variation in density of total activity (den_{jklmn}); feeding activity as a proportion of total activity did not differ among these strata.

Density of grizzly bear locations. — We used radiotelemetry locations of marked bears directly to estimate total density of bear activity in each habitat type by season, year type, edge type, and area, controlling for the effects of proximity to roads and major human facilities. We used data from 1976 to 1992.

We calculated relative density of total activity (den_{jklmn}) as the quotient of estimated proportional use of different spatial strata by radio-marked bears (u_{jklmn}) divided by the proportional area of each stratum (a_{kmn}): $den_{jklmn} = u_{jklmn} / a_{kmn}$. We calculated proportional use, by season and year type, as: $u_{jklmn} = [a_{kmn} / (1 - p_{jklmn})] - a_{kmn}$, where p_{jklmn} was the probability that a location would be that of a telemetered radio-marked bear versus a random point. This expression is equivalent to the odds that a location would occur in a given stratum. Probabilities (p_{jklmn}) were back-calculated from logits ($p = e^{\text{logit}} / (1 - e^{\text{logit}})$) that were modeled as dependent responses in analysis-of-covariance on categories (Demaris, 1992).

We considered the effects of habitat type, forest/nonforest edge, distance to the nearest road, distance to the nearest major human development, and, for spring only, winter range in the development of statistical models. Habitat type, edge (≤100 m versus >100 m), and winter range (bison, wapiti, and neither) were categorical variables. Distances to nearest road and human development were covariates. We used roads of all types specified in the Yellowstone grizzly bear cumulative effects model database, whereas we defined major human developments as any concentration of human activity that included ≥30 facilities (e.g., houses) or the capacity for ≥100 persons to overnight within a 1-km-radius circular area. In most models these human-related effects were expressed as second- and third-order polynomials. We calculated logit-transformed probabilites of bear activity, used to calculate densities, from models where human-related effects were set to zero. We developed different models for each season, year type, and region, as well as different models for areas within regions that were with and without substantial year-round bison populations heavily used by grizzly bears. We selected models on the basis of minimizing Akaike's Information Criterion (AIC) (Sakamoto, 1991; Burnham and Anderson, 1998), except that we constrained all models to include habitat type.

We weighted frequencies of random points so that they summed to the total of bear locations used in each model (Manly and others, 1992). The resulting beta coefficients approximately equaled zero when modeled frequency of bear use equaled the frequency of random points in a given stratum. A coefficient ≈ 0 corresponded to $p \approx 0.5$ and $den \approx 1$ (i.e., the odds that a location would have been from a telemetered bear equaled the odds that it would have been a random point). This

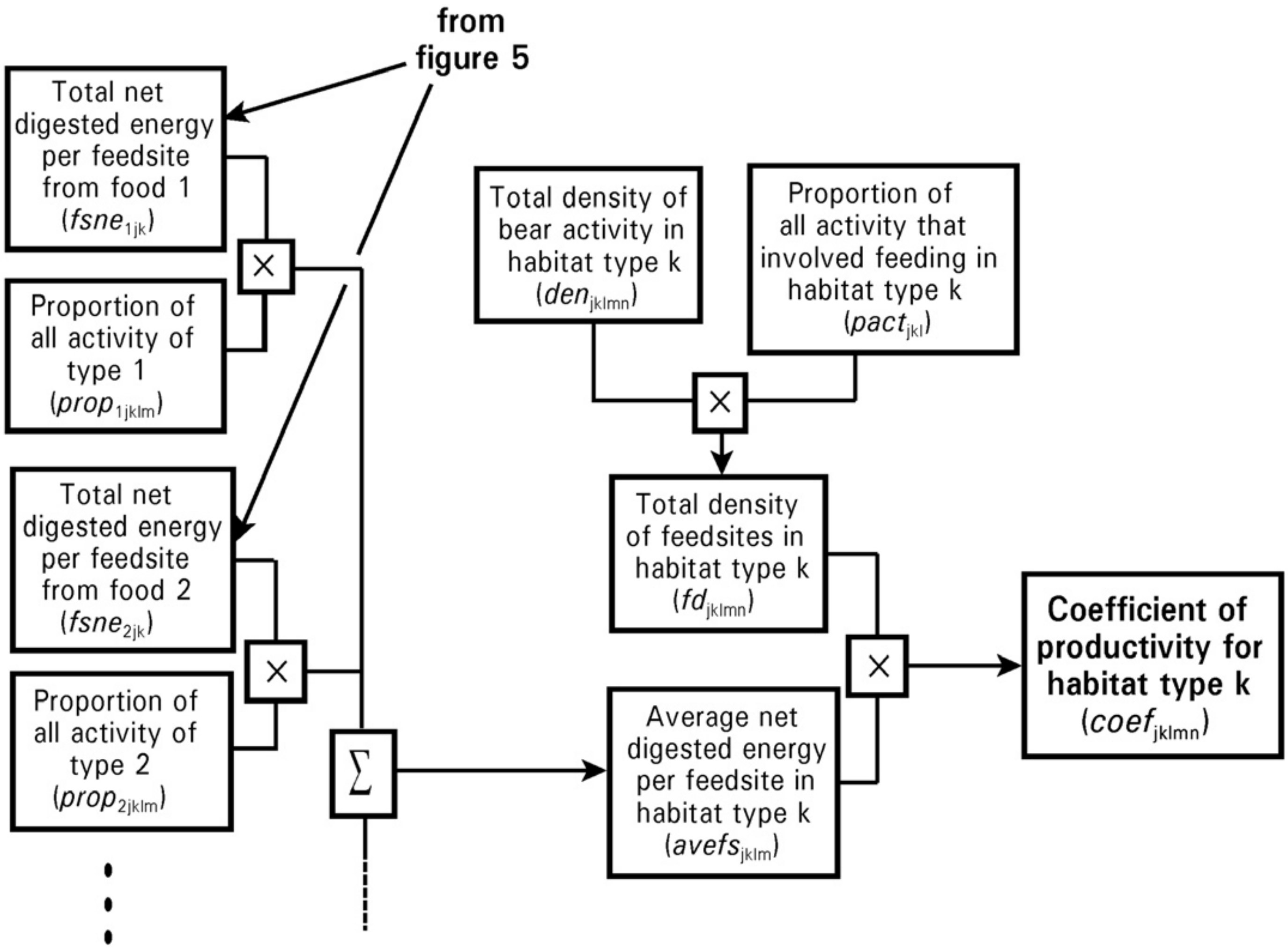

Figure 6. Schematic for the final calculation of productivity for habitat type k ($coef_{jklmn}$), for Yellowstone grizzly bears.

structure allowed us to easily compare results among models, but it also implicitly assumed that density of bear use was equal among seasons, year types, and regions. This assumption is reasonable when comparing seasons and year types within regions but questionable when comparing among regions. Densities of grizzly bears probably differed among regions in the Yellowstone ecosystem as a function of differences in overall habitat productivity (Mattson, 1987; Blanchard and others, 1992).

We subsumed changes in proportional areas of habitat types and forest/nonforest edge that were attributable to the 1988 fires in procedures for calculating a_{kmn}. Prefire and postfire habitat type and edge identifications were assigned to random points proportional to the bear sample that was pre- and postburn in each ecosystem region. This was done by generating a random variable with a uniform distribution ranging from 0 to 1. Random points with values greater than or equal to the proportion of bear locations obtained after the 1988 fires were assigned a postfire coefficient. Random points with values less than the proportion of bear locations prefire were assigned prefire coefficients. This procedure allowed us to use prefire and postfire bear data without separate prefire and postfire models for each temporal and spatial stratum. Sample sizes of bear locations were too small to support what would otherwise have been an additional permutation of models.

Proportion of bear locations with feeding activity. — We estimated the proportion of bear locations at which feeding activity occurred ($pact_{jkl}$) for each season j, habitat type k, and year type l. We used only observations that were obtained from locations of radio-marked bears. This approach reduced sample sizes by approximately one-half compared to our analysis of the proportional distribution of feeding activities (see "Average Net Energy Digested per Feedsite by Habitat Type," p. 15). These small sample sizes prevented us from estimating proportional levels of feeding activity for each region and edge type. We also combined year types within seasons for this calculation when sample sizes for both year type categories were too small.

We adjusted total density to reflect the proportional occurrence of feeding activity because our analysis focused on the extraction of energy from different landscape units by Yellowstone grizzly bears rather than on density of bear activity. Many telemetry locations were associated with bears either traveling or resting (Mattson, 1997a). These types of activities undoubtedly engendered energetic costs and benefits. Such gains or losses are difficult to quantify, however, and are likely to be a small fraction of a grizzly bear's energetic budget during the active season (Fancy and White, 1985).

Coefficients

We calculated coefficients ($coef_{\mathrm{jklmn}}$) for assessing the productivity of Yellowstone's grizzly bear habitat for each temporal and spatial stratum as the product of density of feeding activity (fd_{jklmn}) times net energy digested per feeding site ($avefs_{\mathrm{jklm}}$): $coef_{\mathrm{jklmn}} = fd_{\mathrm{jklmn}} \times avefs_{\mathrm{jklm}}$ (fig. 6). Variation in $coef_{\mathrm{jklmn}}$ between edge types was due only to variation in density of feedsites; net digested energy per feedsite did not differ for this stratification. These coefficients of productivity directly reflect the net energy that bears derive from an area, accounting for the energetic benefits of foods that were consumed and the energetic costs of extracting those foods once found. They do not reflect the energetic costs of search and travel or the energetic benefits of favorable microclimates. Coefficients are in units that have temporal and spatial specificity so that they can be summed over units of time and space. However, coefficient values are still indicative rather than absolute measures of net energetic gain, primarily because the measure of energy expenditure is an index and also because there are not explicit estimates of the total food derived from a given type at a given time. Coefficients have additional value in that the fraction of energy gained from different feeding activities or foods can be specified for each stratum and for areas to which the coefficients are applied so that judgements can be made regarding the relative importance of different feeding activities or foods.

Coefficients for Army Cutworm Moth and Cutthroat Trout Feeding Sites

Grizzly bear use of aggregated army cutworm moths and spawning cutthroat trout was singular with regards to our research sampling efforts in the Yellowstone ecosystem. These activities were undersampled in the ecosystem-wide effort because they were, to a unique extent, highly localized around highly productive sites (Mattson and others, 1991b; Mattson and Reinhart, 1995). For this reason, we took a tailored approach to estimating coefficients for these activities and others associated with habitat complexes around moth aggregation sites and trout spawning streams. These coefficients supercede all other coefficients within specified zones-of-influence (ZOIs).

Our rationale for calculating moth and trout ZOI coefficients was the same as described in preceding sections, except that some data were different. Calculations of net digested energy were the same. Overall density of grizzly bear activity was analyzed for composite ranges of bears known to use these two foods. We treated the ratio of observed to expected levels of use for ZOIs within these composite ranges as the analogue of relative density (Mattson and others, 1991b; Mattson and Reinhart, 1995). In fact, this treatment is directly comparable to densities calculated, as described above, with random locations weighted to total the number of bear locations used in each model. We defined the extent of zones-of-influence as the point where levels of proportional use first equaled levels of proportional availability within 500-m intervals successively farther away from aggregation sites or streams (Mattson and others, 1987; Mattson and others, 1991b; Mattson and Reinhart, 1995). No moth sites were located near enough to roads or major human developments to be affected by bears avoiding these features (Mattson and others, 1991b; O'Brien and Lindzey, 1994). Some spawning streams were located near human facilities (Reinhart and Mattson, 1990), but we assumed that the effect of bears underusing streams near humans would be offset by bears overusing more remote streams when considering the entire spectrum of streams around Yellowstone Lake (Reinhart and Mattson, 1990).

We reduced densities of bear locations near moth sites or spawning streams to reflect only feeding activity. We based this on the proportion of time bears were observed to be feeding by direct visual observation (French and French, 1990; O'Brien and Lindzey, 1994; Mattson and Reinhart, 1995; White, 1996). We calculated average feedsite values using the proportions of food items in the diets of bears that used habitat complexes associated with these two foods. We estimated these diets from analyses of feces collected within each habitat

Cutthroat trout (left) and army cutworm moths (above) are major grizzly bear foods in certain regions of the Yellowstone ecosystem. Bears consume cutthroat trout in spawning streams tributary to Yellowstone Lake and army cutworm moths at high elevations in the Absaroka Mountains to the east (trout photo by Daniel Reinhart, National Park Service; moth photo by Jeff Henry, Roche Jaune Pictures).

complex (Mattson and others, 1991b; Mattson and Reinhart, 1995) and corrected to account for detection- and digestion-related biases (Hewitt and Robbins, 1996).

Results

Net Energy Digested per Gram of Ingested Food

Nutrient content of foods consumed by Yellowstone grizzly bears varied considerably within and among seasons (table 8). Percent crude protein content varied 20 times between stems of flowering elk thistles and the tissue of ungulates during spring. Protein content of clovers and graminoids consumed by bears declined with progression of the growing season, and for graminoids, protein content averaged one-half of spring values during late hyperphagia. In general, crude protein content was much higher for animal foods than for plant foods. Among plant foods, crude fiber content varied by six times and was lowest in roots and highest in graminoids, horsetail, and elk thistle. Ash content was high in horsetail because of its high silica content (Cody and Wagner, 1981), and also high in pondweed roots, mushrooms, and pocket gopher root caches. Fat content was singularly high in army cutworm moths, followed by late season ungulate tissue, ants, and whitebark pine seeds.

Estimated mean percent digestibility of energy in foods consumed by Yellowstone grizzly bears was nearly as variable as nutrient contents (table 9). Digestibility varied five- to sevenfold, from a low of 19% for elk thistle and 13% for late season graminoids to a high of 95% for cutthroat trout (Pritchard and Robbins, 1990). In general, the energy in vertebrates was most digestible, followed by energy in invertebrates and roots. Of foliage grazed by bears, energy contained in clover, spring beauty, dandelions, and fireweed was most available to bears.

As would be expected, the average dry weight of foods varied depending on the units that were used to measure consumption by grizzly bears (tables 10–12). Among foods where consumption was calculated in terms of bite size, volumes of graminoid and clover increased commensurate to plant growth during the active season and reached a maximum with horsetail and late season consumption of clover. These maximum bite sizes (0.54 g for horsetail and 0.44 g for clover) were similar to the asymptotic bite size estimated for grizzly bears consuming fresh alfalfa (0.64 g) (Gross and others, 1993b). Conversely, bite sizes of spring beauty were quite small because of the dispersed nature and small size of spring beauty stems. Excluding spring beauty, bite sizes of fruits (0.15 g–0.60 g) were similar to those of grazed foods (0.12 g–0.54 g). Among root foods, individual roots of biscuitroots were larger, on average, than individual roots of yampa or sweet-cicely. However, judged on the basis of cubic decimeters of excavation, differences were minimal between yampa and biscuitroot because, on average, more than one yampa root was excavated per dig. On a per cubic decimeter basis, bears obtained more of yampa and biscuitroot than sweet-cicely or pondweed roots. Finally, invertebrates were the smallest units of food: all were <0.1 g per individual.


Biscuitroots excavated from a grizzly bear feeding site in northern Yellowstone National Park. Biscuitroots are frequently consumed by grizzly bears, especially on wind swept ridges in northern and eastern parts of the Yellowstone ecosystem (photo by David Mattson, U.S. Geological Survey).

Mean resistances (kilograms) of matrix material to excavation varied sixfold depending on the season and type of matrix (table 13). On average, resistance was least for dirt and debris hills constructed by ants and was greatest late in the growing season for soils enclosing yampa roots. Even so, difficulty of excavation was quite similar for a number of activities, including the excavation of roots early in the growing season, the excavation of cones from middens, the excavation of ants from logs, and the excavation of mushrooms from forest floor debris.

Relative net energy digested per gram of ingested food accounted for digestive efficiencies and the energetic costs of extracting a bite from a surrounding matrix or shearing it from contiguous tissue such as leaf or stem (Appendix 4). This measure did not account for metabolic efficiencies or costs of search among and within sites. This measure also reflects the energetics of a subset of sites and foods that were selected out of all of those available for exploitation by bears. For example, the net digested energy associated with grazing clover during late hyperphagia only applies to those few patches of clover

Table 8. Mean percent moisture-free nutrient content of foods consumed by grizzly bears in the Yellowstone ecosystem, 1987-92.

[(-) denotes a situation where SD could not be calculated because n=1]

Food	Percent crude protein			Percent crude fiber			Percent ash			Percent starch		
	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*
Graminoids												
Spring	**20.7**	(4.8)	*24*	**21.2**	(3.9)	*24*	**10.2**	(2.0)	*16*			
Estrus	**20.1**	(5.4)	*36*	**23.0**	(4.6)	*37*	**9.1**	(1.6)	*28*			
Early hyperphagia	**15.0**	(3.1)	*5*	**29.4**	(5.9)	*5*	**7.8**	(1.2)	*4*			
Late hyperphagia	**9.0**	(5.8)	*4*	**31.2**	(4.0)	*4*	**9.4**	(2.5)	*4*			
Clover												
Spring	**25.7**	(2.0)	*4*	**12.6**	(1.3)	*4*	**10.1**	(2.1)	*2*			
Estrus	**21.5**	(2.7)	*8*	**16.7**	(6.1)	*8*	**15.4**	(5.0)	*6*			
Early hyperphagia	**20.3**	(3.3)	*7*	**19.2**	(4.2)	*7*	**9.8**	(2.2)	*4*			
Dandelion	**19.2**	(6.7)	*2*	**14.0**	(5.2)	*2*	**17.4**	(7.2)	*2*			
Fireweed												
Estrus	**15.8**	(-)	*1*	**17.1**	(-)	*1*	**8.4**	(-)	*1*			
Early hyperphagia	**23.0**	(4.5)	*3*	**10.7**	(2.0)	*3*	**9.2**	(1.0)	*3*			
Horsetail	**13.3**	(5.6)	*26*	**20.8**	(4.8)	*27*	**21.7**	(4.7)	*24*			
Spring beauty	**25.4**	(5.8)	*11*	**13.7**	(3.3)	*12*	**14.2**	(2.2)	*10*			
Elk thistle	**4.1**	(1.6)	*16*	**27.8**	(4.5)	*16*	**15.2**	(3.2)	*16*			
Mushroom	**17.8**	(5.1)	*4*	**12.6**	(2.8)	*4*	**18.0**	(9.6)	*4*			
Pocket gopher cache	**8.6**	(2.9)	*8*	**10.8**	(3.6)	*8*	**18.3**	(8.2)	*8*	**5.0**	(3.0)	*10*
Vole cache	**5.1**	(-)	*1*	**5.2**	(-)	*1*	**4.9**	(-)	*1*	**8.3**	(-)	*1*
Pondweed root	**8.7**	(0.6)	*2*	**6.4**	(0.7)	*2*	**25.9**	(7.5)	*2*	**28.5**	(11.8)	*5*
Yampa root	**5.9**	(1.7)	*26*	**6.5**	(2.7)	*27*	**6.6**	(4.4)	*23*	**36.3**	(11.0)	*57*
Sweet-cicely root	**7.8**	(1.5)	*4*	**13.2**	(5.0)	*4*	**7.8**	(7.8)	*4*	**27.8**	(20.9)	*11*
Biscuitroot root	**5.2**	(1.4)	*34*	**9.5**	(2.5)	*34*	**11.4**	(6.4)	*34*	**31.7**	(11.1)	*69*
										Percent fat		
Ant	**36.8**	(-)	*1*	**18.3**[e]			**6.1**[e]			**32.5**[e]		
Wapiti[a]												
Spring and Estrus	**80**						**4**			**18**		
Early hyperphagia	**62**						**4**			**36**		
Late hyperphagia	**45**						**4**			**53**		
Bison and moose[a]												
Spring and Estrus	**81**						**2**			**15**		
Early hyperphagia	**67**						**2**			**29**		
Late hyperphagia	**53**						**2**			**43**		
Cutthroat trout[b]	**69.6**						**9.3**			**17.5**		
Army cutworm moths[c]	**34.2**									**64.0**		
Whitebark pine seed[d]	**12.8**			**34.8**			**2.2**			**27.1**		

[a] From information in Mitchell and others, 1976; Anderson, 1981; Bubenik, 1982; Robbins, 1983; Berger and Peacock, 1988; Pritchard and Robbins, 1990; Pond and Ramsay, 1992; Mattson, 1997b.

[b] From Pritchard and Robbins, 1990.

[c] From O'Brien and Lindzey, 1994; White, 1996.

[d] From Mattson and Reinhart, 1994.

[e] From Ogborn, 1990; Noyce and others, 1997.

Table 9. Estimated mean percent digestibility of energy in foods consumed by grizzly bears in the Yellowstone ecosystem, 1987-92.

Food	Year-round			Spring			Estrus			Early hyperphagia			Late hyperphagia		
	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*
Stems															
Graminoids foliage[a]				**33.9**	(8.1)	*24*	**31.4**	(9.1)	*37*	**17.5**	(12.4)	*5*	**13.0**	(8.0)	*4*
Clover foliage[a]				**52.8**	(3.5)	*4*	**42.7**	(12.0)	*8*	**38.6**	(8.4)	*7*	**46.8**	(8.9)	*2*
Dandelion foliage and flower	**45.6**	(5.8)	*46*												
Fireweed foliage[a]							**43.6**	(-)	*1*	**56.9**	(4.6)	*3*			
Horsetail stem	**32.0**	(8.6)	*27*												
Spring beauty foliage and flower	**48.7**	(7.4)	*12*												
Elk thistle stem	**18.8**	(11.2)	*16*												
Mushroom basidiocarp	**51.1**	(4.5)	*4*												
Roots															
Pocket gopher root cache	**47.9**	(18.6)	*10*												
Vole root cache	**71.5**	(-)	*1*												
Pondweed root	**68.4**	(8.6)	*5*												
Yampa root[b]	**71.8**	(8.0)	*57*												
Sweet-cicely root	**63.6**	(14.2)	*11*												
Biscuitroot root[b]	**63.3**	(8.7)	*69*												
Whitebark pine seeds[d]	**49.4**														
Ant adults	**57.2**	(-)	*1*												
Army cutworm moths[c]	**75**														
Ungulates[d]															
Wapiti				**90**			**90**			**92**			**93**		
Bison & moose				**92**			**92**			**94**			**96**		
Cutthroat trout[d]	**94.5**														

[a] Means differed ($\alpha = 0.10$) by season and between bear feeding sites and monitoring plots. Only samples from feeding sites were used.

[b] Means differed between bear feeding sites and random plots. Only samples from feeding sites were used.

[c] From O'Brien and Lindzey, 1994.

[d] From Pritchard and Robbins, 1990.

used by bears, presumably because of desirable nutritional characteristics. Digested energy was typically highest for ungulates followed by insects, fruits, seeds, roots, and grazed foods. Considering the costs of extraction, ungulates remained the energetically most valuable food. A large number of root, fruit, and seed foods clustered together at intermediate values, followed by most grazed foods, insects (excluding army cutworm moths), rodents, and rodent food caches. The net energetic value of insects dropped dramatically from that associated only with digestive efficiencies because of the often high costs of extraction coupled with the small size of rewards. Exceptions to these generalities included ants from dirt and debris hills, which exhibited a high value because of typically large colony sizes and ease of excavation; voles during spring and estrus, because of the preponderance of meat in the reward; and fireweed during hyperphagia.

Coefficients of Habitat Productivity

The factors given in Appendix 5 were used to convert units of activity observed at grizzly bear activity sites to units of mass (grams) that could be compared among different seasons and types of feeding activity. These values reflect not only the amount of food obtained per unit activity but also

Table 10. Basis for estimates of nutrient content for ungulates and army cutworm moths and of digestibility for ungulates used in calculation of coefficients of habitat productivity for Yellowstone grizzly bears.

Assumption or calculation	Reference or source
Wapiti during late hyperphagia were ascribed the protein and fat composition of deer.	Pritchard and Robbins, 1990
Bison and moose during late hyperphagia were ascribed the protein and fat composition of cattle.	Pritchard and Robbins, 1990
Edible fractions of the carcass (ebw) were calculated as: ebw = live weight (lw) – skeletal weight – rumen weight – water weight.	Mattson, 1997b
Differences between fall and spring or late winter ebw (ebw_{fall} and ebw_{spring}, respectively) were attributed to loss of body fat.	
Change in ebw from fall to spring ($\Delta\ ebw$) was standardized as: $\Delta\ ebw = (ebw_{fall} - ebw_{spring})/ebw_{fall}$; where ebw_{spring} was recalculated based on percent or absolute changes in lw from fall to spring obtained from the listed references.	Mitchell and others, 1976; Anderson, 1981; Bubenik, 1982; Berger and Peacock, 1988
Percent ebw_{spring} protein ($protein_{spring}$) was calculated as: $protein_{spring} = 100 \times (protein_{fall}/[100 - \%\ \text{ash} - \Delta\ ebw])$	
Percent ebw_{spring} fat (fat_{spring}) was calculated as: $fat_{spring} = (100\% - \text{ash}) - protein_{spring}$	
Nutrient fractions of moths were calculated as the average of two studies, using the average for each study of values obtained after August 1.	O'Brien and Lindzey, 1994; White, 1996
Animal fat was assumed to be ca. 99% digestible, ash and total dietary fiber not digestible, and protein ($dprot$) digestible according to percent of protein ($protein$) in the carcass as: $dprot = 3.82 + 1.01\ protein$.	Pritchard and Robbins, 1990

different probabilities of detection associated with different foraging behaviors. For example, the very low values associated with yampa and biscuitroot reflect not only the small reward per dig (i.e., roughly one root) but also the likelihood that root excavations are more often documented in comparison to activities such as grazing because of the prominence and durability of the associated sign. By contrast, the large values for grazed foods reflect the many bites represented by a single feces (the unit of activity for grazing), as well as the lower probabilities of detection associated with grazing, which is a relatively cryptic behavior. These conversion factors therefore contain information pertaining to the behavior of bears and the characteristics of their foods as well as the biases introduced during the sampling process. Mean levels of activity specific to each food and type (Appendix 6) were multiplied by the conversion factors to obtain mean relative net energy per feedsite ($fsne_{ijk}$) (Appendix 7). Because this calculation controlled for sampling bias, values in Appendix 7 should be interpreted as conveying information about the energy obtained per feedsite and as correcting for biases introduced during sampling.

The proportion of grizzly bear locations where feeding signs were observed varied considerably among habitat types and seasons (Appendix 8). Feeding activity was proportionally more common in most types during early and late hyperphagia compared to spring and estrus. This escalation was to be expected since early and late hyperphagic seasons were defined on the basis of previously documented increases in feeding activity (see table 4). Feeding activity was also proportionally more common during all seasons in nonforest types compared to forest types. This prevalence of feeding versus other activities was especially evident for lithic ridges (habitat type 4), mesic grasslands and meadows (habitat type 6), marshes, fens, and wet meadows (habitat types 5 and 8).

Relative density of feeding activity (Appendix 9) was multiplied times the mean energetic value of a feedsite (Appendix 10) to obtain coefficients of habitat productivity (Appendix 11) for each habitat type, year type, season, and region. Examined separately, relative density and mean feedsite value provide insight into the seasonal foraging environment of different habitat types. For example, density of feeding activity was typically high but mean energetic value of feedsites was low in mesic grasslands and meadows (habitat type 6). This example characterizes a foraging environment with numerous predictable low to moderate quality feeding opportunities that attract considerable bear use. By contrast, some habitat types such as mesic subalpine fir forests (habitat type 10701) were characterized by relatively low densities of

Table 11. Average dry weight (in grams) obtained by grizzly bears per feeding unit (e.g., bite, root, excavation, food cache, stem) at feeding sites in the Yellowstone ecosystem, 1986-92.

[Samples size (*n*) denotes number of sites; within-site sample sizes varied from 5 to >100, depending on the food]

Food	Year-round			Spring			Estrus			Early hyperphagia			Late hyperphagia		
	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*
Graminoids (per bite)[a]				**0.14**	(0.04)	*18*	**0.20**	(0.11)	*14*	**0.30**	(0.16)	*5*			
Clover (per bite)[a]				**0.21**	(0.07)	*5*	**0.22**	(0.13)	*9*	**0.44**	(0.26)	*17*			
Dandelion (per bite)	**0.33**	(0.34)	*11*												
Fireweed (per bite)	**0.28**	(-)	*1*												
Alpine clover (per bite)	**0.12**	(0.04)	*3*												
Horsetail (per bite)	**0.54**	(-)	*1*												
Spring beauty (per stem)	**0.03**	(0.01)	*9*	(assuming 1.5 stems per bite, bite size = 0.05)											
Elk thistle (per stem)	**4.9**	(2.1)	*14*												
Mushrooms (per basidiocarp)	**7.6**	(5.0)	*3*												
Rodent root cache (per cache)	**37.8**	(32.5)	*12*												
Earthworms (per excavated cubic decimeter)	**1.1**	(-)	*1*												
Pondweed root (per excavated cubic decimeter)	**0.25**	(0.12)	*6*												
Yampa															
(per root)[a]				**0.21**	(0.05)	*3*	**0.57**	(0.28)	*14*	**0.49**	(0.17)	*54*	**0.54**	(0.10)	*5*
(roots per excavation)	**1.6**	(0.52)	*96*												
(cubic decimeters per excavation)	**2.0**	(1.0)	*20*												
Sweet-cicely															
(per root)	**0.60**	(0.38)	*14*												
(roots per excavation)	**3.3**	(4.8)	*12*												
(cubic decimeters per excavation)	**9.2**	(16.6)	*12*												
Biscuitroot															
(per root)	**0.89**	(0.41)	*104*												
(cubic decimeters per excavation)	**2.3**	(2.4)	*28*												

[a] Means differed ($\alpha = 0.10$) by season.

Table 12. Estimated dry weights of grizzly bear foods not sampled during this study. Values were obtained from the referenced literature.

Food	Dry weight (grams)	Assumptions	References
Cutthroat trout	**47.3**	75% body water, 42% consumption	Mattson and Reinhart, 1994
Adult pocket gopher	**22.0**		Hansen and Bear, 1964 Hansen and Reid, 1973
Pocket gopher litter	**3.5**	0.7 g per neonate, 5 neonates per litter	Hansen and Bear, 1964 Anderson and MacMahon, 1981 Chase and others, 1982
Adult vole	**5.8**	78% body water	Pitts and Bullard, 1968 Campbell and Dobson, 1992
Vole litter	**1.1**	0.2 g per neonate, 5.5 neonates per litter	Pinter, 1979
Earthworm	**0.062**	85% body water	Lawrence and Millar, 1945 Grant, 1955 Lee, 1985
Ants per log	**1.7**	75% body water, body mass and colony sizes of representative species	Brian, 1978 Peakin and Josen, 1978
Ants per hill	**4.7**	As per above and 25% utilization, based on mean percent excavation per nest = 41 ± 21 (n = 143)	
Ants per rock	**0.1**	As per above	
Hornet nest	**1.4**	10 mg per hornet and 25% utilization	Akre and others, 1980 Redford and Dorea, 1984
Army cutworm moth	**0.09**	7% body water	O'Brien and Lindzey, 1994 White, 1996
Fleshy fruit (per bite)			
Globe huckleberry	**0.60**	1.5 berries per bite	Welch and others, 1997
Buffaloberry	**0.32**	As above	
Strawberry	**0.30**	As above and assuming 0.2 g per fruit	
Grouse whortleberry	**0.15**	As above and comparable in size to *Vaccinium vitis-idaea*	Ross and LaRoi, 1990
Whitebark pine seeds (per cone)	**7.2**	80 seeds per cone, 0.09 g per seed	Mattson and Reinhart, 1994

feeding activity, with high average feedsite value, especially during spring. This pattern suggests a patchy and unpredictable environment, with potentially substantial rewards. As another contrast, dry nonforest areas (habitat type 2) typically supported low densities of feeding activity that were of low to moderate value, whereas the whitebark pine type (habitat type 10201) supported high densities of high-value feeding activity during hyperphagia.

In most habitat types, much of the mean productivity per feedsite (as distinct from total productivity) was associated with consumption of ungulates (figs. 7–9). This was especially the case for wet nonforest (habitat types 5 and 8), mesic and dry forest openings (habitat types 10600 and 10100), Douglas-fir types (habitat types 10301 and 10801), low elevation spruce (habitat type 10601), and low elevation lodgepole pine (habitat type 10501). Dry, lithic, and mesic nonforest types (habitat types 2, 4, and 6) derived much of their value from root foods, while whitebark pine and subalpine fir types (habitat types 10201, 10101, and 10701) derived much or most of their value from whitebark pine seeds. The same is true for forests dominated by grouse whortleberry (habitat type 10401), depending on whether bison were or were not present in substantial numbers. In areas with substantial numbers of bison, peak productivity was shifted from spring or late hyperphagia to estrus or early hyperphagia. This shift reflected grizzly bear use of bison that died either from injuries sustained during the rut (early hyperphagia) or trauma associated with calving (spring and estrus) (Green and others, 1997; Mattson, 1997b).

Final coefficients in Appendix 11 are presented by habitat type, season, year type, and region, and by location in or out of forest/nonforest edge. Coefficients in Appendix 12 are averaged over year types. In regions where a type was so sparse that a coefficient could not be estimated, values were assigned

Table 13. Mean (SD) values (in kilograms) obtained from a claw-o-meter used to excavate grizzly bear feeding sites in a way that simulated the observed bear signs, Yellowstone ecosystem, 1987-92.

[Values represent averages for sites based on 10 samples per site; sample size (*n*) denotes number of sites. Excavations averaged 2.2 ± 1.9 dm^3 (*n* = 48) in size]

Feeding activity	Year-round			Estrus			Early hyperphagia			Late hyperphagia		
	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*	$\bar{x}$	(SD)	*n*
Excavating squirrel middens (pine seeds)	**11.7**	(9.0)	*14*									
Excavating mushrooms	**9.1**	(13.9)	*3*									
Excavating logs (ants)	**13.3**	(11.9)	*15*									
Excavating debris hills (ants)	**4.7**	(3.6)	*3*									
Excavating rodent nests and caches	**6.6**	(10.5)	*14*									
Excavating yampa roots[a]				**9.9**	(9.9)	*6*	**19.9**	(15.4)	*21*	**27.4**	(21.4)	*3*
Excavating biscuitroot roots[a]				**9.7**	(20.6)	*14*	**15.9**	(17.4)	*17*	**16.1**	(21.4)	*10*

[a] Means differed ($\alpha = 0.10$) by season.

to it from the next most similar type. This circumstance occurred in most regions for habitat types 4 and 7, 10301 and 10801, and 10101 and 10201. Only in the east were values estimated separately for types 10101 and 10301. The west and east were the only regions where coefficients were estimated for ungulate winter ranges during spring; the west was the only region with coefficients estimated for bison winter range. Bear Management Units were distinguished as being with and without bison, year-long, only in the south and west. This distinction was not made for the north because there is little evidence that grizzly bears in this region made substantial use of the relatively numerous resident bison (Green and others, 1997; Mattson, 1997b). Even so, the use of bison that did occur in this region is reflected in the associated coefficients.

Coefficients for ZOIs associated with army cutworm moth aggregation sites and cutthroat trout spawning streams are presented in table 14 along with supporting information for their calculation. These ZOI coefficients are roughly two times the maximum value of any coefficient associated with a specific habitat type. Cutworm moths and trout provide a high concentration of net digested energy, similar to that of ungulates. The food sources and feeding activity associated with these ZOIs are also highly concentrated. Although of relatively limited extent, these ZOIs predictably constitute “ecocenters” of habitat productivity (Craighead and others, 1995).

Discussion

Applying the Coefficients

For maximum comparability among analysis areas, coefficients should be weighted by the proportional area of the spatial strata to which they apply. A weighted summation across types yields a unit area average productivity for the analysis area. Such a value is useful for most spatial and temporal comparisons because (1) the effects of differences in the spatial extent of different analysis areas are eliminated and (2) the calculated value is of a magnitude better suited to human cognition than those values obtained by absolute area-weighted summations. Total productivity can be easily obtained by multiplying average productivity by total area.

The spatial resolution of grizzly bear habitat productivity should correspond to the temporal resolution and associated time-specific uncertainty of the coefficients. Coefficients are specific only to season and are therefore generalized at that scale with respect to time units such as weeks, days, or hours. In other words, the coefficients represent a probabilistic statement within the span of a season regarding anything that might happen during a time period of shorter duration. Seasonal range sizes constitute the obvious spatial resolution corresponding to seasonal coefficients. Given that seasonal grizzly bear ranges in the Yellowstone ecosystem are about 50 times larger than the resolution of habitat mapping for the Yellowstone grizzly bear CEM (about 100 km^2 compared to 2 ha), some method needs to be employed to generalize productivity-attributed CEM maps to a scale that matches seasonal grizzly bear movements, especially for purposes of display.

This type of generalization is most logically achieved by focal-area analysis. Such an approach entails calculating average productivity for a seasonal-range-sized area, or “window,” and applying that average value to the focal cell (centroid). This is repeated for each cell of the map base. The resulting generalized “surface” of productivity is considerably smoothed relative to any representation of raw values used in the calculation. Intuitively, such a smoothed output is a more plausible representation of seasonally averaged productivity. This kind of smoothing is especially important for purposes of display.

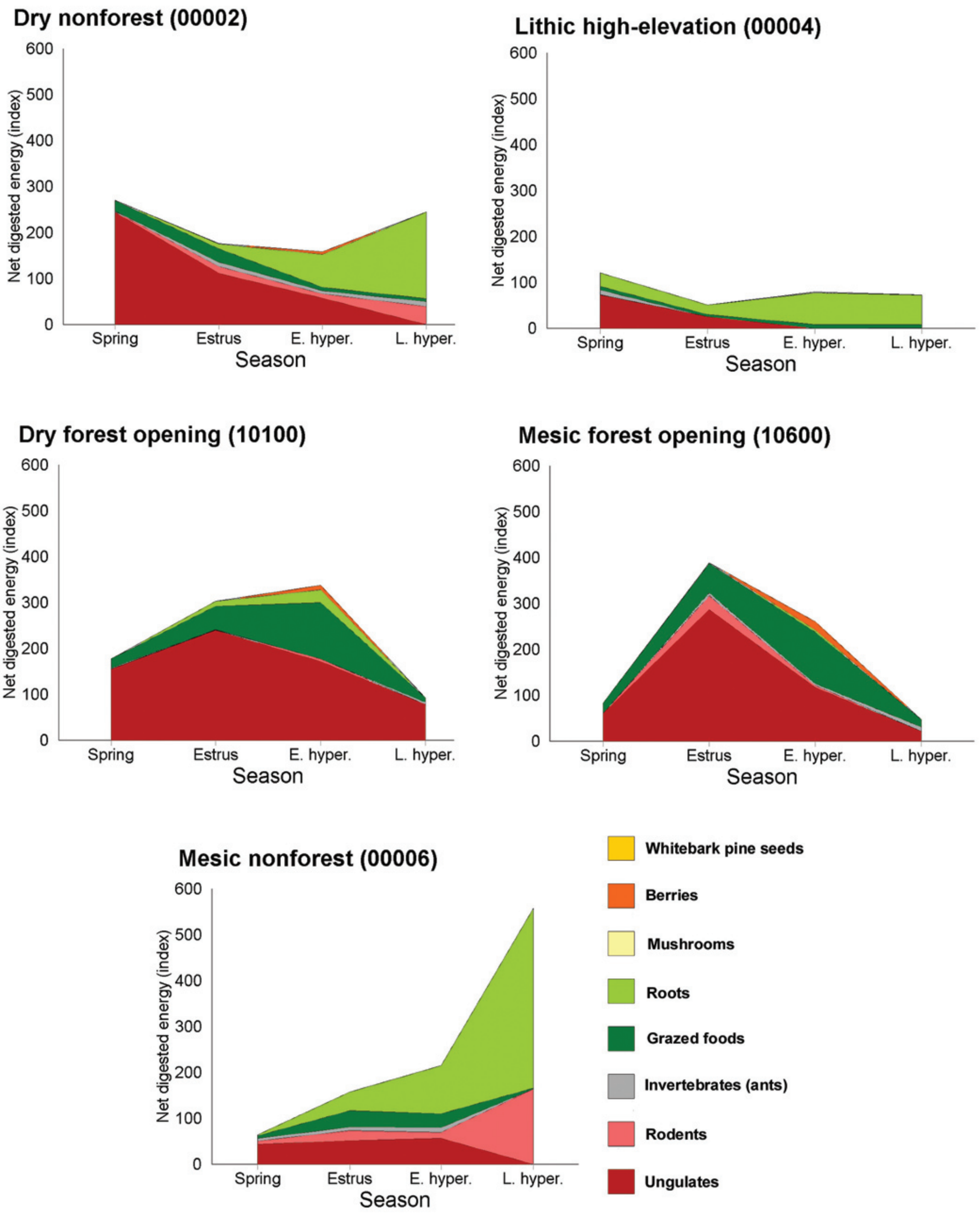

Figure 7. Fractions of mean seasonal feedsite value attributable to broad classes of grizzly bear foods in the Yellowstone ecosystem for five nonforest habitat types. Names and codes are given for each habitat type; E. hyper. = early hyperphagia, and L. hyper. = late hyperphagia.

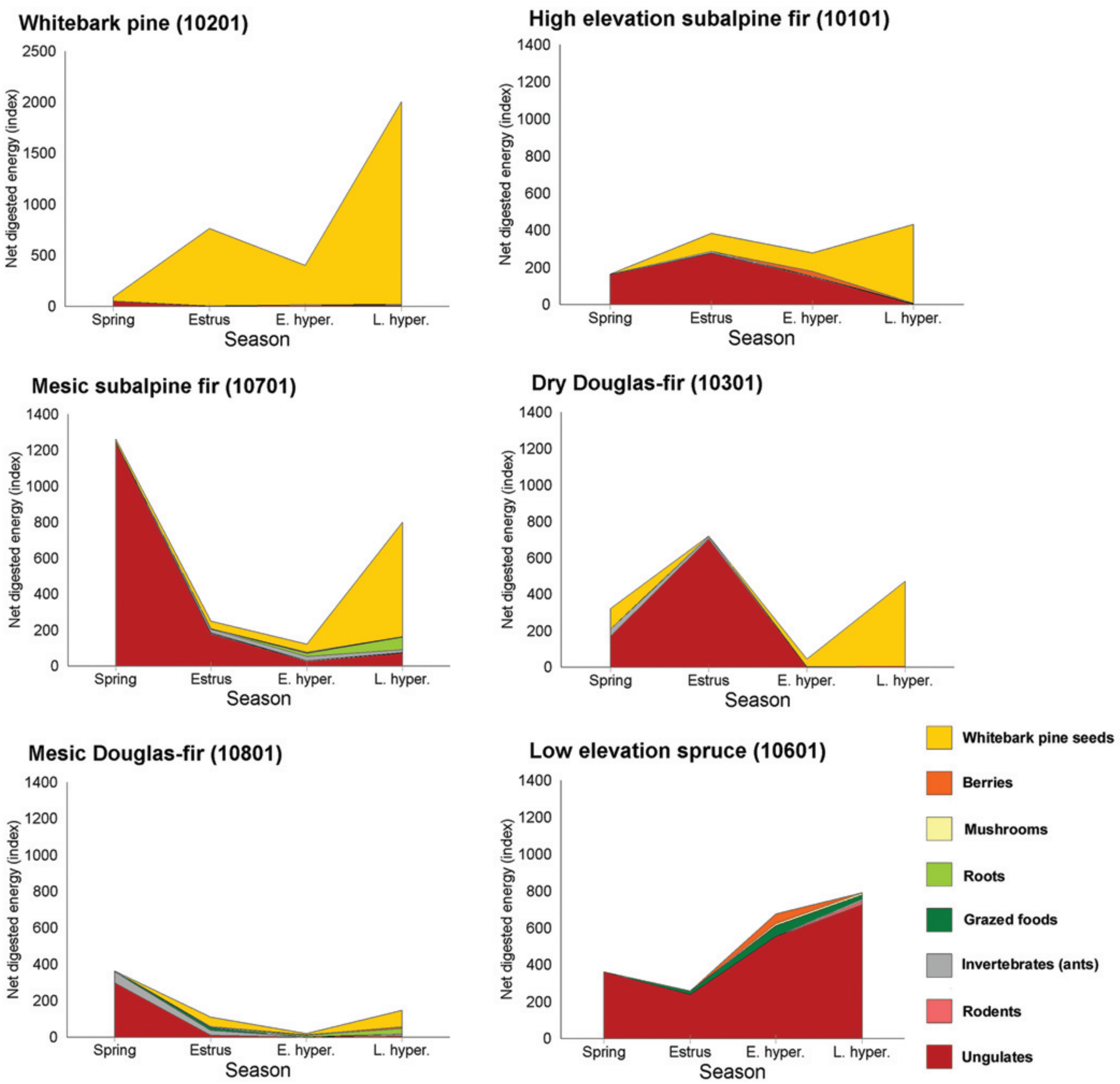

Figure 8. Fractions of mean seasonal feedsite value attributable to broad classes of grizzly bear foods in the Yellowstone ecosystem for six forest habitat types. Names and codes are given for each habitat type; E. hyper. = early hyperphagia, and L. hyper. = late hyperphagia.

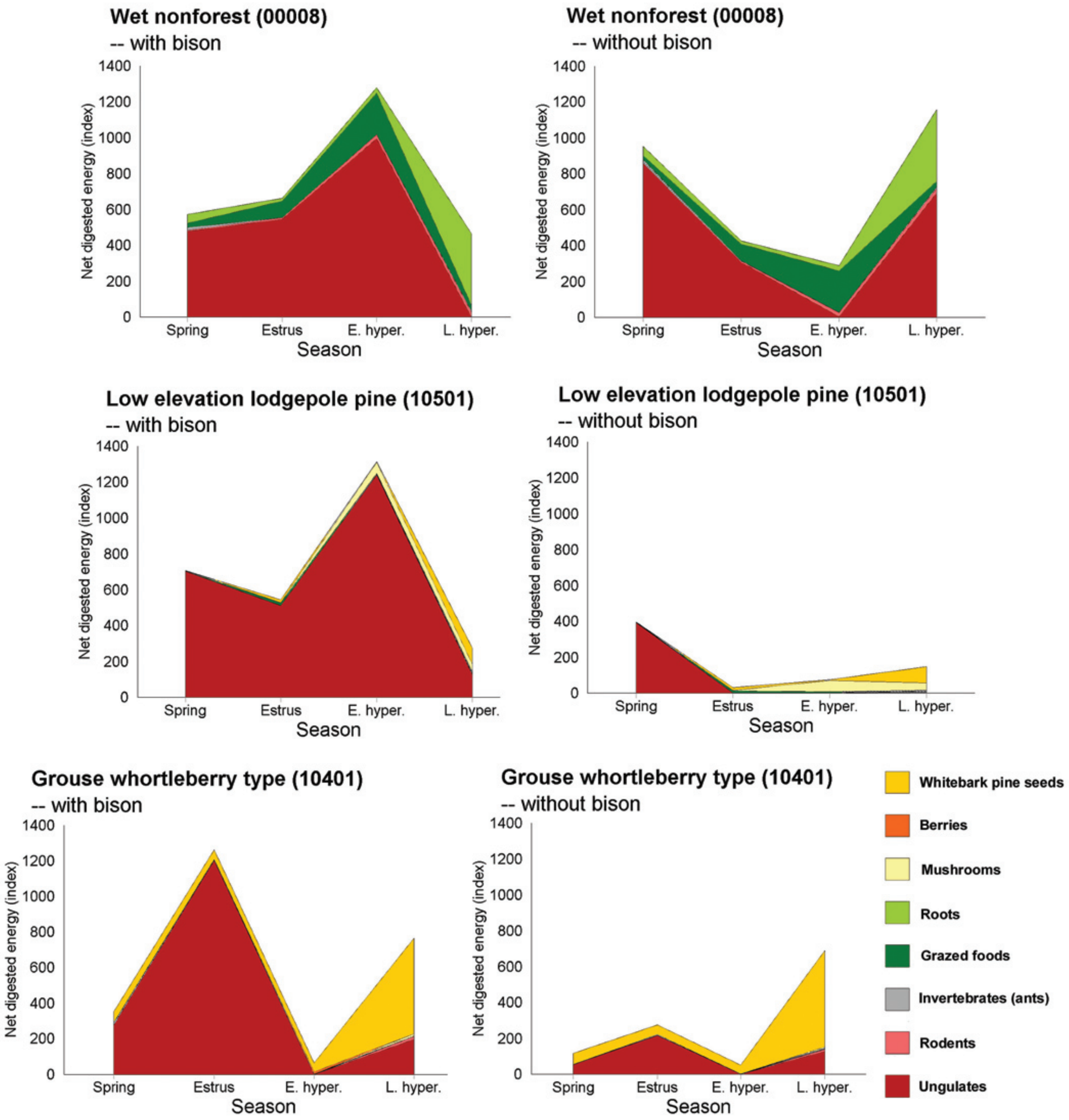

Figure 9. Fractions of mean seasonal feedsite value attributable to broad classes of grizzly bear foods in the Yellowstone ecosystem for three habitat types distinguished by whether they occur in areas with or without substantial use of bison by grizzly bears. Names and codes are given for each habitat type; E. hyper. = early hyperphagia, and L. hyper. = late hyperphagia.

For some purposes, productivity may best be displayed by categories. Five-part categories were determined based on quintiles for untransformed or natural-log transformed distributions, as appropriate, of raw values and values generated by focal area analysis. These categories are described in table 15.

Region-specific coefficients are designed to apply to all BMUs within the region, regardless of whether those units were used in derivations. A good match to BMUs #12, #13, and #18 on the western edge of the ecosystem has yet to be determined. If coefficients are applied outside of the current Yellowstone recovery area, a set should be selected from the region, by season, within the recovery area that most closely matches the conditions of the extralimital analysis area. Finding such a match from within the recovery area will be most problematic for areas that produce substantial amounts of fruits. Consumption of fruits is not well-represented by the coefficients because the Yellowstone ecosystem is notable for its lack of berries and the related consumption of them by grizzly bears (Mattson and others, 1991a).

Interpreting the Coefficients

As discussed in the "Methods" section, these coefficients are a partial accounting of the net digested energy obtained by Yellowstone grizzly bears from different habitat types, accounting for the effects of season, type of year, region, winter range, and proximity to forest/nonforest edge. Coefficient values are relative insofar as the estimate of expended energy is expressed as an index and total production of net energy is not tallied for lack of a comprehensive census of bear activity. Coefficient values also directly reflect the exhibited behavior of grizzly bears at any given time and place, specifically in terms of the quality and quantity of food that was ingested. Coefficients reflect the availability of foods within any given temporal or spatial strata only to the extent that these attributes are reflected in grizzly bear foraging activity. In essence, the approach taken here has the decided advantage of directly capturing information regarding the choices that bears make in their acceptance or rejection of foods and foraging patches.

These coefficients account primarily for energetic costs at the level of the bite. They do not account for the costs of search and travel within or among feeding sites. Even so, costs of search and travel were accounted for to the extent that these nonfeeding activities did not contribute to calculated habitat type values. This indirect accounting of nonfeeding costs implicitly assumes that these costs did not differ among types. There has been no test of this assumption, but there is evidence that travel through forest stands or harvest units with substantial amounts of undergrowth and coarse woody debris is more costly for bears than travel in open conditions (Smith, 1978; Mattson, 1997a). Even so, it is unclear how much energy such

Table 14. Parameters for calculating and applying coefficients ($coef_{jklmn}$) associated with army cutworm moth and cutthroat trout feeding areas in the Yellowstone grizzly bear cumulative effects model.

Parameter	Feeding area type	
	Army cutworm moth aggregation sites	**Cutthroat trout spawning streams**
Season of application	Early hyperphagia	Estrus
Zones-of-influence (kilometer radius)	Mapped polygon + 500 m buffer	2.0
(A) Relative density of bear activity	12.1	9.7
(B) Proportion of time feeding	0.67	0.30
(C) Relative density of feeding activity[a]	8.1	2.9
(D) Net digested energy per gram (kilocalories)	4.62	4.50
(E) Grams ingested per feedsite	367	1234
(F) Net kcal digested per feedsite[b]	1361[d] 1594[e]	5268
Coefficient[c]	11024[d] 12911[e]	15277
Sources	Pritchard and Robbins, 1990 Mattson and others, 1991b French and others, 1994 O'Brien and Lindzey, 1994 White, 1996 Kevan and Kendall, 1997	Pritchard and Robbins, 1990 French and French, 1990 Mattson and Reinhart, 1994

[a] A × B

[b] D × E

[c] C × F

[d] For WBP = Y years.

[e] For WBP = N years.

Table 15. Five-part categories for displaying raw and smoothed productivity values for Yellowstone grizzly bear habitat.

[“Scale” refers to whether transformed or untransformed values were used to define categories. “ln” refers to natural-log transformed. “Range” refers to the total range of values. “Min-max” refers to the range of values for each category]

Spring			Estrus			Early hyperphagia			Late hyperphagia		
Scale	Range	Min-max	Scale	Range	Min-max	Scale	Range	Min-max	Scale	Range	Min-max
Raw values											
ln	5-500	**0-13**	ln	5-750	**0-14**	ln	5-1000	**0-14**	ln	5-3000	**0-18**
		14-32			**15-37**			**15-42**			**19-65**
		33-80			**38-100**			**43-120**			**66-233**
		81-200			**101-275**			**121-350**			**234-835**
		200+			**275+**			**350+**			**835+**
Smoothed values											
ln	5-500	**0-13**	Untrans.	5-750	**0-14**	Untrans.	5-1000	**0-14**	ln	5-3000	**0-18**
		14-32			**15-37**			**15-42**			**19-65**
		33-80			**38-100**			**43-120**			**66-233**
		81-200			**101-275**			**121-350**			**234-835**
		200+			**275+**			**350+**			**835+**

differences in travel-related cost might entail, with the possibility that these costs are a relatively small fraction of a grizzly bear's energetic budget (see Hainsworth and Wolf, 1979; Pyke, 1984; Fancy and White, 1985; Grünbaum, 1998). Such is likely to be the case if, as all evidence suggests, grizzly bears possess a sophisticated memory and related cognitive map of travel routes and foraging opportunities (Schleyer and others, 1984; Haroldson and Mattson, 1985; Harting, 1985). Under such circumstances, travel to potential foraging sites would be relatively efficient. Within a site, an increasing body of evidence suggests that bite size (and quality) more than food density, per se, largely governs rate of intake and associated energetics (Gross and others, 1993a, 1993b; Mattson, 1997c; Welch and others, 1997). By implication, within-site costs of search may be negligible compared to the costs of handling food. Thus, it is likely that energetic considerations at the level of the bite are, indeed, the most critical.

Coefficient values have unit area and unit time specificity and can therefore be summed over time and space. They also can be explicitly compared among seasons and types of years, assuming that there are equal numbers of bears in a given BMU during different seasons and years. Coefficients can be compared among regions, but only assuming that density of bear activity is equal. As mentioned before, this assumption is dubious but subject to remedy if and when reliable estimates of bear density are obtained for ecosystem regions where the bear population is locally at or near carrying capacity. With this information, region-specific coefficients can be weighted by region-specific bear densities and can therefore allow for comparison of values among regions without assuming that densities of bear activity are equal.

Yellowstone CEM Coefficients in Context

A number of models have been developed for appraising the suitability, capability, or productivity of bear habitat. These models fall into three basic categories: (1) those based on the abundance of bear foods, often weighted by some ranking of their relative quality (e.g., energy content and digestibility) or acceptance by bears (e.g., Craighead and others, 1982; Hadden and others, 1986; Mace, 1986; Mace and Bissell, 1986; Hamilton and Bunnell, 1987; Kansas and Raine, 1990; Noyce and Coy, 1990; Powell and Seaman, 1990; Costello and Sage, 1994); (2) those based directly on exhibited univariate selection of vegetation types or other natural features (e.g., Schoen and others, 1994); and (3) those based on multivariate or multivariable analyses of habitat selection, including human-related effects such as those of roads (e.g., Clark and others 1993; Mace and others, 1997). Several models of the first type have been tested by comparing food-based values with levels of selection exhibited by radio-marked bears (e.g., Hamilton and Bunnell, 1987; Kansas and Raine, 1990; Costello and Sage, 1994). Such comparisons implicitly test the assumption that digested energy, or some related quality, is the sole determinant of habitat use by bears (Hamilton and Bunnell, 1987). Models of the second and third types assume that the probability or level of bear activity within a given spatial stratum is the primary factor of interest to managers. The energetics of bear activity are not a consideration.

We developed Yellowstone grizzly bear CEM coefficients so as to include as much information as possible, not just about when bears used a site but also about what they were doing there. We emphasized letting the bears inform the model as much as possible regarding what foods they chose to eat, when and where they ate, the quality of those foods, and the per bite expense of feeding. This level of empiricism was possible because, to our knowledge, nowhere else has the full suite of information required for such calculations been collected for a bear population. The approach described here is unique compared to previous models of bear habitat because we incorporate information on bear distributions expressed as relative densities, in contrast to indices of selection or relative probabilities of location. We introduce some degree of control for the effects of proximity to townsites and roads on the behavior of bears as well as the behavior of researchers sampling the bears. We also incorporate information on the amount and quality of food consumed by bears, in contrast to information on the amount and quality of food that was available. This last distinction is important because, as mentioned above, bears exercise a significant level of choice in their use of foods and habitats that may or may not reflect what is considered to be available or preferable by a researcher (Hamilton and Bunnell, 1987; Kansas and Raine, 1990; Costello and Sage, 1994).

Additional Issues and Areas of Future Research

Much of the information germane to these calculations comes from grizzly bear signs encountered at or on route to and from radio-telemetry locations. We likely oversampled feeding activity at lower elevations and nearer roads because greater time was spent there by field crews. We likely undersampled grazing during feedsite examinations because grazing is difficult to detect (Mattson, 1997a). Both of these potential biases were either not relevant to the analysis or were mitigated in calculations. We used feedsites to specify the proportion of activity within habitat types. We did not use them to determine overall density of activity. This latter estimate was based on radio-telemetry locations, which were modeled so as to control for the effects of proximity to roads and other major human facilities. Because habitat types are distributed primarily by elevation (Pfister and others, 1977; Mueggler and Stewart, 1980; Steele and others, 1983), as are roads and human facilities in the Yellowstone ecosystem (Mattson and others, 1987, 1992), the calculation of proportional feeding activity within types was predictably little affected by oversampling feedsites nearer roads. As discussed above (see "Results: Coefficients of Habitat Productivity," p. 21), we used feces to correct for the bias towards undersampling grazing activities. If anything, grazed foods were probably overrepresented by feces (see following paragraph). Conversion factors based on fecal content ($cfctr_{ij}$) not only converted the different units by which feeding activity was measured to the common currency of grams but also, to some extent, corrected for different probabilities of detection among different feeding activities.

The content of feces is an important part of the calculations upon which the Yellowstone grizzly bear CEM coefficients are founded. Much of the critical information needed to convert fecal contents to an estimate of ingested biomass is available (Hewitt and Robbins, 1996). We know little, however, about biases affecting the detection and collection of feces, especially how these biases relate to feces of different compositions. Preliminary analysis of Yellowstone data suggests that feces comprising the remains of pure meat are substantially underrepresented because they are ephemeral, difficult to detect, and often aggregated. By contrast, feces containing ants or grazed foods are probably overrepresented because such feces are large, durable, and often deposited along travel routes. Consequently, the current coefficients probably underrepresent grizzly bear use of meat (i.e., ungulates) and overrepresent the use of ants and grazed foods. Even so, because energy from ants and graminoids currently makes only a minimal contribution to coefficient values, any changes that may arise from further investigation of this issue would probably have little effect on overall results.

Other important information that we used to calculate the coefficients remains weak or speculative. In particular, bite sizes associated with the consumption of meat need better documentation. Of importance to calculating net digested energy from cutthroat trout, the proportion of time spent feeding and the rate of consumption during that time are highly uncertain because of small sample sizes. Additional information on these parameters would be important to future revisions of coefficients. Information also needs to be collected on the energy expended during grazing and during the use of ungulates, ideally in terms that are comparable to existing estimates of resistance to excavation. In general, a method for directly and unambiguously estimating energy expenditure specific to the use of different foods is needed. More data on all parameters used in calculations would be beneficial and would allow for greater temporal and spatial specificity.

The issue of error propagation through multiple operations on multiple estimates is of consequence to a reductionistic approach such as this one. There are several ways that the magnitude and nature of this error can be appraised. One expedient means is to determine whether the coefficients and the derivative analyses are broadly consistent with the results of other research. For example, the large fraction of energy obtained from roots in the lithic high-elevation and mesic nonforest types (fig. 7) is consistent with the concentration of feeding on roots in these habitats (Haroldson and Mattson, 1985; Mattson, 1997c). The large fraction of energy obtained from ungulates in the majority of types is similarly consistent with the large fraction of energy estimated to be contributed by this food to the diet of Yellowstone's grizzly bears (figs. 7–9; Mattson and others, 1991a; Mattson, 1997b; Jacoby and others, 1999), as is the case with the large amounts of energy obtained from whitebark pine seeds in the whitebark pine type (fig. 8; Mattson and others, 1991a, 1994; Mattson and Reinhart, 1994; Felicetti and others, 2003). Further plausible tests of this nature could involve comparing calculations of energy obtained from ungulates, army cutworm moths, and cutthroat trout for different regions with the estimated importance of these foods by Mattson (1997b), Mattson and others (1991b), Reinhart and Mattson (1990), and Mattson and Reinhart (1995). Similarly, patterns of productivity associated with radio-telemetry locations of different genders, ages, and reproductive classes could be tested for consistency with expectations based on parallel ongoing research (Mattson, 2000). These patterns also could be tested for consistency between the radio-telemetry locations that were used to derive the coefficients, from 1977 to 1992, and radio-telemetry locations collected since then.

Sensitivity analysis is an obvious next step for appraising the relative importance of different variables used to calculate the coefficients and the consequent importance of error and uncertainty in each. Sensitivity analysis can be approached several ways, none of which are mutually exclusive. Values for each variable can be set at the mean of relevant strata, and an aggregate change in coefficients can be calculated, such as change in seasonal habitat productivity for representative BMUs. The range of values for each variable can be symmetrically extended around the mean by some fixed percent and change in coefficients similarly calculated. Finally, variables identified as being highly uncertain or potentially highly influential (e.g., proportion of time spent fishing and catch rate for cutthroat trout and factors for converting units of activity to grams ingested [$cfctr_{ij}$]) could be set at the extremes of a biologically plausible range of values.

Additional information on compensatory changes in grizzly bear foraging behavior is desirable if CEM coefficients are to be used to project or otherwise anticipate habitat change. Grizzly bears exhibit a high degree of dietary flexibility in the Yellowstone ecosystem (Mattson and others, 1991a), presumably in response to changes in the relative quality and quantity of foods. For example, use of cutthroat trout and army cutworm moths increased substantially during the 1970s and 1980s, apparently commensurate to increases in abundance of these two foods (Reinhart and Mattson, 1990; Mattson and others, 1991b). Grizzly bears also use more ungulates during the summer and fall of years when whitebark pine seeds are scarce (Mattson, 1997b). Whereas diminishment in any currently important food will likely result in diminished use by grizzly bears, it is unclear to what extent bears can compensate by reverting to extant alternate foods. It is also unclear what foods might increase in abundance. These factors are germane to representing future conditions that might arise from the loss of cutthroat trout, army cutworm moths, or whitebark pine. The mere reduction or increase of landscape features in future projections coupled with static CEM coefficients can only be a crude representation of potential consequences arising from the effects of disease, climate change, or introduced predators. Because of these limitations, future projections should consider a range of possible compensatory responses operationalized either by changes in the extent of map units or changes in the coefficients themselves.

Acknowledgments

Many people contributed to the collection of data used in this analysis. Dan Reinhart, Gerry Green, Roger Swalley, Jeff Henry, and Erin Shannahan contributed substantially to studies of grizzly bear habitat use and activities. Mark Haroldson, Bart Schleyer, and Jamie Jonkel were especially important in trapping and marking bears. Dave Stradley made major contributions as pilot and observer during radio-relocation flights. Funding and other support for this analysis was provided by the U.S. Forest Service, Shoshone National Forest, the USGS Forest and Rangeland Ecosystem Science Center, and the USGS Southwest Biological Science Center. Charles Schwartz, Mark Haroldson, Steve Cherry, and Steve Cain of the Interagency Grizzly Bear Study Team and Barrie Gilbert of Utah State University provided reviews that were much appreciated. Ron Kirby and Ruth Jacobs of the USGS Forest and Rangeland Ecosystem Science Center provided support for completion and publication of this work.

References Cited

Akre, R.D., Greene, A., MacDonald, J.F., Landolt, P.J., and Davis, H.G., 1980, Yellowjackets of America north of Mexico: U.S. Department of Agriculture, Agriculture Handbook No. 552, 102 p.

Anderson, A.E., 1981, Morphological and physiological characteristics, *in* Wallmo, O.C., ed., Mule and black-tailed deer of North America: Lincoln, Nebr., University of Nebraska Press, p. 27-98.

Anderson, D.C., and MacMahon, J.A., 1981, Population dynamics and bioenergetics of a fossorial herbivore, *Thomomys talpoides* (Rodentia: Geomyidae), in a spruce-fir sere: Ecological Monographs, v. 51, p. 179-202.

Berger, J., and Peacock, M., 1988, Variability in size-weight relationships of *Bison bison*: Journal of Mammalogy, v. 69, p. 618-624.

Blanchard, B.M., 1978, Grizzly bear distribution in relation to habitat areas and recreational use: Cabin Creek - Hilgard Mountains: Bozeman, Mont., Montana State University, M.S. thesis, 75 p.

Blanchard, B.M., 1983, Grizzly bear— habitat relationships in the Yellowstone area: International Conference on Bear Research and Management, v. 5, p. 118-123.

Blanchard, B.M., and Knight, R.R., 1991, Movements of Yellowstone grizzly bears: Biological Conservation, v. 58, p. 41-67.

Blanchard, B.M., Knight, R.R., and Mattson, D.J., 1992, Distribution of Yellowstone grizzly bears during the 1980s: American Midland Naturalist, v. 128, p. 332-338.

Brian, M.V., ed., 1978, Production ecology of ants and termites: Cambridge, U.K., Cambridge University Press, 407 p.

Bubenik, A.B., 1982, Physiology, *in* Thomas, J.W., and Toweill, D.E., eds., Elk of North America: Harrisburg, Penn., Stackpole Books, p. 125-180.

Burnham, K.P., and Anderson, D.R., 1998, Model selection strategy and inference: a practical information-theoretic approach: New York, N.Y., Springer, 353 p.

Campbell, M.T., and Dobson, F.S., 1992, Growth and size in meadow voles (*Microtus pennsylvanicus*): American Midland Naturalist, v. 128, p. 180-190.

Chase, J.D., Howard, W.E., and Roseberry, J.T., 1982, Pocket gophers, *in* Chapman, J.A., and Feldhamer, G.A., eds., Wild mammals of North America: Baltimore, Md., The Johns Hopkins University Press, p. 239-255.

Clark, J.D., Dunn, J.E., and Smith, K.G., 1993, A multivariate model of female black bear use for a geographic information system: Journal of Wildlife Management, v. 57, p. 519-526.

Cody, W.J., and Wagner, V., 1981, The biology of Canadian weeds, 49, *Equisetum arvense* L: Canadian Journal of Plant Science, v. 61, p. 123-133.

Costello, C.M., and Sage, R.W., Jr., 1994, Predicting black bear habitat selection from food abundance under 3 forest management systems: International Conference on Bear Research and Management, v. 9, p. 375-387.

Craighead, J.J., Sumner, J.S., and Mitchell, J.A., 1995, The grizzly bears of Yellowstone: Washington, D.C., Island Press, 535 p.

Craighead, J.J., Sumner, J.S., and Scaggs, G.B., 1982, A definitive system for analysis of grizzly bear habitat and other wilderness resources: Missoula, Mont., Wildlife-Wildlands Monograph No. 1, U of M Foundation, University of Montana, 279 p.

Demaris, A., 1992, Logit modeling: practical applications: Newbury Park, Calif., Sage Publications, 87 p.

Despain, D.G., 1990, Yellowstone vegetation: Boulder, Colo., Robert Reinharts, 239 p.

Dixon, B.G., 1997, Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem: Bozeman, Mont., Montana State University, M.S. thesis, 192 p.

Fancy, S.G., and White, R.G., 1985, Incremental cost of activity, *in* Hudson, R.J., and White, R.G., eds., Bioenergetics of wild herbivores: Boca Raton, Fla., CRC Press, p. 143-159.

Felicetti, L.A., Schwartz, C.C., Rye, R.O., Haroldson, M.A., Gunther, K.A., Phillips, D.L., and Robbins, C.T., 2003, Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears: Canadian Journal of Zoology, v. 81, p. 763-770.

French, S.P., and French, M.G., 1990, Comments about bear use of spawning streams in the Bridge Bay-Lake-Fishing Bridge complex: Evanston, Wyo., Yellowstone Grizzly Bear Foundation, 5 p.

French, S.P., French, M.G., and Knight, R.R., 1994, Grizzly bear use of army cutworm moths in the Yellowstone ecosystem: International Conference on Bear Research and Management, v. 9, p. 389-400.

Graham, D.C., 1978, Grizzly bear distribution, use of habitats, food habits and habitat characterization in Pelican and Hayden Valleys, Yellowstone National Park: Bozeman, Mont., Montana State University, M.S. thesis, 88 p.

Grant, W.C., Jr., 1955, Studies on moisture relationships in earthworms: Ecology, v. 36, p. 400-407.

Greater Yellowstone Coordinating Committee, 1987, The greater Yellowstone area: an aggregation of National Park and National Forest management plans: USDI National Park Service, USDA National Forest Service, 241 p.

Green, G.I., Mattson, D.J., and Peek, J.M., 1997, Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park: Journal of Wildlife Management, v. 61, p. 1040-1055.

Gross, J.E., Hobbs, N.T., and Wunder, B.A., 1993a, Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size?: Oikos, v. 68, p. 75-81.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E., and Wunder, B.A., 1993b, Functional response of herbivores in food-concentrated patches: test of a mechanistic model: Ecology, v. 74, p. 778-791.

Grünbaum, D., 1998, Using spatially explicit models to characterize foraging performance in heterogeneous landscapes: American Naturalist, v. 151, p. 97-115.

Gunther, K.A., and Renkin, R.A., 1990, Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986-88: International Conference of Bear Research and Management, v. 8, p. 335-342.

Hadden, D.A., Hann, W.J., and Jonkel, C.J., 1986, An ecological taxonomy for evaluating grizzly bear habitat in the Whitefish Range of Montana, *in* Contreras, G.P., and Evans, K.E., compilers, Proceedings — grizzly bear habitat symposium: USDA Forest Service General Technical Report INT-207, p. 67-77.

Hainsworth, F.R., and Wolf, L.L., 1979, Feeding: an ecological approach: Advances in the Study of Behavior, v. 9, p. 53-96.

Hamer, D., and Herrero, S., 1987, Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta: International Conference on Bear Research and Management, v. 7, p. 199-214.

Hamilton, A.N., and Bunnell, F.L., 1987, Foraging strategies of coastal grizzly bears in the Kimsquit River Valley, British Columbia: International Conference on Bear Research and Management, v. 7, p. 187-197.

Hansen, R.M., and Bear, G.D., 1964, Comparison of pocket gophers from alpine, subalpine and shrub-grassland habitats: Journal of Mammalogy, v. 45, p. 638-640.

Hansen, R.M., and Reid, V.H., 1973, Distributions and adaptations of pocket gophers, *in* Turner, G.T., Hansen, V.H., Reid, V.H., Tietjen, H.P., and Ward, A.L., eds., Pocket gophers and Colorado mountain rangeland: Colorado State University Experiment Station Bulletin 554S, p. 1-19.

Haroldson, M., and Mattson, D.J., 1985, Response of grizzly bears to backcountry human use in Yellowstone National Park: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team Report, 38 p.

Harting, A.L., 1985, Relationships between activity patterns and foraging strategies of Yellowstone grizzly bears: Bozeman, Mont., Montana State University, M.S. thesis, 103 p.

Hewitt, D.G., and Robbins, C.T., 1996, Estimating grizzly bear food habits from fecal analysis: Wildlife Society Bulletin, v. 24, p. 547-550.

Holcroft, A.C., and Herrero, S., 1984, Grizzly bear digging sites for *Hedysarum sulphurescens* roots in southwestern Alberta: Canadian Journal of Zoology, v. 62, p. 2571-2575.

Hudson, R.J., and Frank, S., 1987, Foraging ecology of bison in aspen boreal habitats: Journal of Range Management, v. 40, p. 71-75.

Jacoby, M.E., Hilderbrand, G.V., Servheen, C., Schwartz, C.C., Arthur, S.M., Hamley, T.A., Robbins, C.T., and Michener, R., 1999, Trophic relations of brown and black bears in several western North American ecosystems: Journal of Wildlife Management, v. 63, p. 921-929.

Kansas, J.L., and Raine, R.M., 1990, Methodology used to assess the relative importance of ecological land classification units to black bears in Banff National Park, Alberta: International Conference on Bear Research and Management, v. 8, p. 155-160.

Kevan, P.G., and Kendall, D.M., 1997, Liquid assets for fat bankers: summer nectivory by migratory moths in the Rocky Mountains, Colorado, U.S.A.: Arctic and Alpine Research, v. 29, p. 478-482.

Knight, R.R., and Eberhardt, L.L., 1985, Population dynamics of Yellowstone grizzly bears: Ecology, v. 66, p. 323-334.

Knight, R.R., Mattson, D.J., and Blanchard, B.M., 1984, Movements and habitat use of Yellowstone grizzly bears: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team Report, 177 p.

Lawrence, R.D., and Millar, H.R., 1945, Protein content of earthworms: Nature (London), v. 155, p. 517.

Lee, K.E., 1985, Earthworms: their ecology and relationships with soils and land use: New York, N.Y., Academic Press, 411 p.

Mace, R.D., 1986, Analysis of grizzly bear habitat in the Bob Marshall Wilderness, Montana, *in* Contreras, G.P., and Evans, K.E., compilers, Proceedings — grizzly bear habitat symposium: USDA Forest Service General Technical Report INT-207, p. 136-149.

Mace, R.D., and Bissell, G.N., 1986, Grizzly bear food resources in the flood plains and avalanche chutes of the Bob Marshall Wilderness, Montana, *in* Contreras, G.P., and Evans, K.E., compilers, Proceedings — grizzly bear habitat symposium: USDA Forest Service General Technical Report INT-207, p. 78-91.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., and Zuring, H., 1997, Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana: Journal of Applied Ecology, v. 33, p. 1395-1404.

Manly, B.F.J., McDonald, L.L., and Thomas, D.L., 1992, Resource selection by animals: London, U.K., Chapman & Hall, 172 p.

Mattson, D.J., 1987, Habitat dynamics and their relationship to biological parameters of the Yellowstone grizzly bear, 1977-83 — progress report: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team, 28 p.

Mattson, D.J., 1991, Field manual for the collection of grizzly bear habitat data in the Yellowstone ecosystem — 1991 revision: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team.

Mattson, D.J., 1997a, Use of lodgepole pine cover types by Yellowstone grizzly bears: Journal of Wildlife Management, v. 61, p. 480-496.

Mattson, D.J., 1997b, Use of ungulates by Yellowstone grizzly bears *Ursus arctos*: Biological Conservation, v. 81, p. 161-177.

Mattson, D.J., 1997c, Selection of microsites by grizzly bears to excavate biscuitroots: Journal of Mammalogy, v. 78, p. 228-238.

Mattson, D.J., 2000, Causes and consequences of dietary differences among Yellowstone grizzly bears *Ursus arctos*: Moscow, Id., University of Idaho, Ph.D. dissertation, 173 p.

Mattson, D.J., 2001, Myrmecophagy by Yellowstone grizzly bears: Canadian Journal of Zoology, v. 79, p. 779-793.

Mattson, D.J., 2004, Exploitation of pocket gophers by grizzly bears: Journal of Mammalogy, v. 85, in press.

Mattson, D.J., Blanchard, B.M., and Knight, R.R., 1991a, Food habits of Yellowstone grizzly bears, 1977-1987: Canadian Journal of Zoology, v. 69, p. 1619-1629.

Mattson, D.J., Blanchard, B.M., and Knight, R.R., 1992, Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops: Journal of Wildlife Management, v. 56, p. 432-442.

Mattson, D.J., and Despain, D.G., 1985, Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem: Yellowstone National Park, Wyo., National Park Service, U.S. Forest Service, 37 p.

Mattson, D.J., Gillin, C.M., Benson, S.A., and Knight, R.R., 1991b, Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem: Canadian Journal of Zoology, v. 69, p. 2430-2435.

Mattson, D.J., Herrero, S., Wright, R.G., and Pease, C.M., 1996, Designing and managing protected areas for grizzly bears: how much is enough?, *in* Wright, R.G., ed., National Parks and protected areas: their role in environmental protection: Cambridge, Mass., Blackwell Science, p. 133-164.

Mattson, D.J., and Jonkel, C., 1990, Stone pines and bears, *in* Schmidt, W.C., and McDonald, K.J., compilers, Proceedings — symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource: U.S. Forest Service General Technical Report INT-270, p. 223-236.

Mattson, D.J., and Knight, R.R., 1989, Evaluation of grizzly bear habitat using habitat and cover type classifications, *in* Ferguson, D.E., Morgan, P., and Johnson, F.D., compilers, Proceedings — land classifications based on vegetation: applications for resource management: U.S. Forest Service General Technical Report INT-257, p. 135-143.

Mattson, D.J., Knight, R.R., and Blanchard, B.M., 1986, Derivation of habitat component values for the Yellowstone grizzly bear, *in* Contreras, G., and Evans, K., compilers, Proceedings — grizzly bear habitat symposium: U.S. Forest Service General Technical Report INT-207, p. 222-229.

Mattson, D.J., Knight, R.R., and Blanchard, B.M., 1987, The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming: International Conference on Bear Research and Management, v. 7, p. 259-273.

Mattson, D.J., and Reinhart, D.P., 1994, Bear use of whitebark pine seeds in North America, *in* Schmidt, W.C., and Holtmeier, F.-K., compilers, Proceedings — international workshop on subalpine stone pines and their environment: the status of our knowledge: U.S. Forest Service General Technical Report INT-GTR-309, p. 212-220.

Mattson, D.J., and Reinhart, D.P., 1995, Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975-1989: Canadian Journal of Zoology, v. 73, p. 2072-2079.

Mattson, D.J., and Reinhart, D.P., 1997, Excavation of red squirrel middens by Yellowstone grizzly bears: Journal of Applied Ecology, v. 34, p. 926-940.

Mattson, D.J., Reinhart, D.P., and Blanchard, B.M., 1994, Variation in production and bear use of whitebark pine seeds in the Yellowstone area, *in* Despain, D.G., ed., Plants and their environments: proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem: National Park Service Technical Report NPS/NRYELL/NRTR, p. 205-220.

Mealey, S.P., 1975, The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973-74: Bozeman, Mont., Montana State University, M.S. thesis, 158 p.

Mitchell, B., McCowan, D., and Nicholson, I.A., 1976, Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*: Journal of Zoology (London), v. 180, p. 107-127.

Mueggler, W.F., and Stewart, W.L., 1980, Grassland and shrubland habitat types of western Montana: USDA Forest Service General Technical Report INT-66, 154 p.

Nelson, R.A., Folk, G.E., Jr., Pfeiffer, E.W., Craighead, J.J., Jonkel, C.J., and Steiger, D.L., 1983, Behavior, biochemistry, and hibernation in black, grizzly, and polar bears: International Conference on Bear Research and Management, v. 5, p. 284-290.

Noyce, K.V., and Coy, P.L., 1990, Abundance and productivity of bear food species in different forest types of northcentral Minnesota: International Conference on Bear Research and Management, v. 8, p. 169-181.

Noyce, K.V., Kannowski, P.B., and Riggs, M.R., 1997, Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota: Canadian Journal of Zoology, v. 75, p. 1671-1686.

O'Brien, S.L., and Lindzey, F.G., 1994, Final report: grizzly bear use of moth aggregation sites and summer ecology of the army cutworm moth in the Absaroka Mountains, Wyoming: Laramie, Wyo., University of Wyoming, Wyoming Cooperative Fish & Wildlife Research Unit, 279 p.

Ogborn, G.L., 1990, Ants (Formicidae) in diet of American black bears (*Ursus americanus*) in southeastern Utah: Provo, Utah, Brigham Young University, M.S. thesis, 15 p.

Peakin, G.J., and Josen, G., 1978, Respiration and energy flow, *in* Brian, M.V., ed., Production ecology of ants and termites: Cambridge, U.K., Cambridge University Press, p. 111-163.

Pease, C.M., and Mattson, D.J., 1999, Demography of the Yellowstone grizzly bears: Ecology, v. 80, p. 957-975.

Pfister, R., Kovalchik, B., Arno, S., and Presby, R., 1977, Forest habitat types of Montana: USDA Forest Service General Technical Report INT-34, 174 p.

Pinter, A.J., 1979, Environmental variables and multiannual cycles in population density of the montane vole, *Microtus montanus*, in Grand Teton National Park — a preliminary report, *in* Linn, R.M., ed., Proceedings of the first conference on scientific research in national parks. Volume 1. National Park Service, Transactions and Proceedings Series, No. 5, p. 279-285.

Pitts, G.C., and Bullard, T.R., 1968, Some interspecific aspects of body composition in mammals, *in* National Academy of Sciences, ed., Body composition in animals and man: Washington, D.C., National Academy of Sciences, p. 45-70.

Pond, C.M., and Ramsay, M.A., 1992, Allometry of the distribution of adipose tissue in Carnivora: Canadian Journal of Zoology, v. 70, p. 342-347.

Powell, R.A., and Seaman, D.E., 1990, Production of important black bear foods in the southern Appalachians: International Conference on Bear Research and Management, v. 8, p. 183-187.

Pritchard, G.T., and Robbins, C.T., 1990, Digestive and metabolic efficiencies of grizzly and black bears: Canadian Journal of Zoology, v. 68, p. 1645-1651.

Pyke, G.H., 1984, Optimal foraging theory: a critical review: Annual Review of Ecology & Systematics, v. 15, p. 523-575.

Redford, K.H., and Dorea, J.G., 1984, The nutritional value of invertebrates with emphasis on ants and termites as food for mammals: Journal of Zoology (London), v. 203, p. 385-395.

Reinhart, D.P., and Mattson, D.J., 1990, Bear use of cutthroat trout spawning streams in Yellowstone National Park: International Conference on Bear Research and Management, v. 8, p. 343-350.

Robbins, C.T., 1983, Wildlife feeding and nutrition: Orlando, Fla., Academic Press, 343 p.

Ross, M.S., and LaRoi, G.H., 1990, Above-ground biomass allocation by four understory vascular plant species in central Alberta jack pine, *Pinus banksiana*, forests: Canadian Field-Naturalist, v. 104, p. 394-402.

Sakamoto, Y., 1991, Categorical data analysis by AIC: Tokyo, Japan, KTK Scientific Publishers, 214 p.

Schleyer, B.O., 1983, Activity patterns of grizzly bears in the Yellowstone ecosystem and their reproductive behavior, predation, and the use of carrion: Bozeman, Mont., Montana State University, M.S. thesis, 130 p.

Schleyer, B., Jonkel, J., Rhoades, K., and Dunbar, D., 1984, The effects of nonmotorized recreation on grizzly bear behavior and habitat use: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team Report, 83 p.

Schmidt-Nielson, K., 1990, Animal physiology: adaptation and environment, fourth edition: New York, N.Y., Cambridge University Press, 602 p.

Schoen, J.W., Flynn, R.W., Suring, L.W., Titus, K., and Beier, L., 1994, Habitat capability model for brown bear in southeast Alaska: International Conference on Bear Research and Management, v. 9, p. 327-337.

Smith, B., 1978, Investigations into black and grizzly bear responses to coastal logging — 1977: Vancouver, B.C., Canada, Simon Fraser University, senior thesis, 85 p.

Steele, R., Cooper, S., Ondov, D., Roberts, D., and Pfister, R., 1983, Forest habitat types of eastern Idaho-western Wyoming: USDA Forest Service General Technical Report INT-144, 122 p.

Stuebe, M.M., and Anderson, D.C., 1985, Nutritional ecology of a fossorial herbivore: protein N and energy value of winter caches made by the northern pocket gopher, *Thomomys talpoides*: Canadian Journal of Zoology, v. 63, p. 1101-1105.

Swift, D.M., 1983, A simulation model of energy and nitrogen balance for free-ranging ruminants: Journal of Wildlife Management, v. 47, p. 620-645.

Weaver, J., Escano, R., Mattson, D., and Puchlerz, T., 1986, Cumulative effects process for the Yellowstone ecosystem, *in* Contreras, G., and Evans, K., compilers, Proceedings — grizzly bear habitat symposium: U.S. Forest Service General Technical Report INT-207, p. 234-246.

Welch, C.A., Keay, J., Kendall, K.C., and Robbins, C.T., 1997, Constraints on frugivory by bears: Ecology, v. 78, p. 1105-1119.

White, D.D., Jr., 1996, Two grizzly bear studies: moth feeding ecology and male reproductive biology: Bozeman, Mont., Montana State University, Ph.D. dissertation, 79 p.

Appendix 1. Common and Scientific Names of Species in this Report

[Scientific names are from the International Taxonomic Information System [ITIS, available at http://itis.usda.gov/index.html] unless those named were found to be in error or unless otherwise noted]

Common name	Scientific name
Animals	
Ants, bees, wasps	Hymenoptera (order)
Army cutworm moth(s)	*Euxoa auxiliaris*
Bison	*Bos bison*
Black bear(s)	*Ursus americanus*
Cutthroat trout	*Oncorhynchus clarki*[1]
Earthworm(s)	Oligochaeta (class)
Grizzly bear(s)	*Ursus arctos*
Ground squirrel(s)	*Spermophilus columbianus*
Moose	*Alces alces*
Mule deer	*Odocoileus hemionus*
Pocket gopher(s)	*Thomomys talpoides*
Red squirrel(s)	*Tamiasciurus hudsonicus*
Rodent(s)	Rodentia (order)
Vole(s)	*Microtus* spp.
Wapiti	*Cervus elaphus*
Wasp(s)	Vespidae (family)
Plants	
Alfalfa	*Medicago sativa*[2]
Alpine avens	*Geum rossii*
Alpine timothy	*Phleum alpinum*
Antelope bitterbrush	*Purshia tridentata*
Arrowleaf groundsel	*Senecio triangularis*
Ballhead sandwort	*Arenaria congesta*
Baltic rush	*Juncus balticus*
Beaked sedge	*Carex rostrata*
Big sagebrush	*Artemisia tridentata*
Biscuitroot(s)	*Lomatium cous*[2]
Bluebunch wheatgrass	*Agropyron spicatum*[2] (*Pseudoroegneria spicata*[4])
Bluegrass	*Poa* spp.
Bluejoint reedgrass	*Calamagrostis canadensis*
Broadleaf arnica	*Arnica latifolia*
Buffaloberry	*Sheperdia canadensis*[2]
Clover	*Trifolium* spp.
Common snowberry	*Symphoricarpos albus*
Common juniper	*Juniperus communis*
Cow parsnip	*Heracleum lanatum*[2] (*Heracleum maximum*[3])
Dandelion	*Taraxacum* spp.
Douglas-fir	*Pseudotsuga menziesii*
Elephanthead lousewort	*Pedicularis groenlandica*
Elk thistle	*Cirsium scariosum*[2]
Elk sedge	*Carex geyerii*
Engelmann spruce	*Picea engelmannii*
Fireweed	*Epilobium angustifolium*[2] (*Chamerion angustifolium*[3])
Geyer willow	*Salix geyeriana*
Globe huckleberry	*Vaccinium globulare*[2] (*Vaccinium membranaceum*[3])
Graminoids	Poaceae and Cyperaceae (families)
Plants, continued	
Grouse whortleberry	*Vaccinium scoparium*
Heartleaf arnica	*Arnica cordifolia*
Horsetail	*Equisetum arvense*
Idaho fescue	*Festuca idahoensis*
Inflated sedge	*Carex vesicaria*
Lingonberry	*Vaccinium vitis-idaea*
Little larkspur	*Delphinium bicolor*
Lodgepole pine	*Pinus contorta*
Mountain snowberry	*Symphoricarpos oreophilus*
Mushroom(s)	Hymenomycetes (class)
Nineleaf biscuitroot	*Lomatium triternatum*
Olney's bulrush	*Scirpus olneyi*[2] (*Schoenoplectus americanus*[3])
Oregon grape	*Berberis repens*[2] (*Mahonia repens*[3])
Ovalhead sedge	*Carex microptera*
Parry's clover	*Trifolium parryi*
Pinegrass	*Calamagrostis rubescens*
Pinyon pine	*Pinus edulis*
Pondweed	*Potamogeton* spp.
Quaking aspen	*Populus tremuloides*
Red baneberry	*Actaea rubra*
Richardson's stipa	*Stipa richardsonii*[2] (*Acnatherum richardsonii*[5])
Ross's sedge	*Carex rossii*
Shrubby cinquefoil	*Potentilla fruticosa*[2] (*Dasiphora floribunda*[3])
Silver sagebrush	*Artemisia cana*
Silvery lupine	*Lupinus argenteus*
Slender wheatgrass	*Agropyron caninum*[2] (*Elymus trachycaulus*[4])
Spring beauty	*Claytonia lanceolata*
Sticky geranium	*Geranium viscosissimum*
Strawberry	*Fragaria* spp.
Subalpine fir	*Abies lasiocarpa*[2] (*Abies bifolia*[6])
Sweet bedstraw	*Galium triflorum*
Sweet-cicely	*Osmorhiza* spp.
Tea-leaved willow	*Salix phylicifolia*[2] (*Salix planifolia*[3])
Thick-leaved wild strawberry	*Fragaria virginiana*
Tufted hairgrass	*Deschampsia caespitosa*
Water sedge	*Carex aquatilis*
Western meadowrue	*Thalictrum occidentale*
Western coneflower	*Rudbeckia occidentalis*
White spirea	*Spiraea betulifolia*
Whitebark pine	*Pinus albicaulis*
Wolf willow	*Salix wolfii*
Yampa	*Perideridia gairdneri*

---

[1] Behnke, 1992.

[2] Hitchcock and Cronquist, 1973.

[3] ITIS.

[4] Barkworth and Dewey, 1985.

[5] Weber and Whittmann, 1996.

[6] Flora of North America Committee, 1993.

Appendix 1 References

Barkworth, M.E., and Dewey, D.R., 1985, Genomically based genera in the perennial Triticeae of North America: identification and membership: American Journal of Botany, v. 72, p. 767-776.

Behnke, R.J., 1992, Native trout of western North America: Bethesda, Md., American Fisheries Society, 275 p.

Flora of North America Committee, ed., 1993, Flora of North America north of Mexico, volume 2: Pteridophytes and Gymnosperms: New York, N.Y., Oxford University Press, 496 p.

Hitchcock, C.L., and Cronquist, A., 1973, Flora of the Pacific Northwest: Seattle, Wash., University of Washington Press, 730 p.

Weber, W.A., and Whittmann, R.C., 1996, Colorado flora: eastern slope, second edition: Niwot, Colo., University Press of Colorado, 524 p.

Appendix 2. Coefficients of Habitat Effectiveness for Yellowstone's Grizzly Bear Habitat

Section 2.1: Background

Grizzly bears exhibit a wide range of tolerances for humans and human facilities. While some bears use only areas remote from humans, others use heavily human-influenced niches, often with humans immediately nearby (Herrero, 1985; Aumiller and Matt, 1994; Mattson and others, 1996). Bears that exhibit extremes of these behaviors are called either wary or habituated. Although a gradient of individual behaviors exists, anecdotes and case histories from the Yellowstone ecosystem suggest that the transition from wariness to habituation can be rapid. Pease and Mattson (1999) show a theoretical exponential increase in levels of habituation to humans among animals that have survived initial contacts. For these reasons, we treated grizzly bears in this analysis as one of two behavioral types (wary or habituated), although we realized that transitional individuals would exhibit intermediate traits (Mattson and others, 1992; Pease and Mattson, 1999).

The relative extent to which grizzly bears use areas near human facilities is likely to be a relative function of the number of habituated animals in a population and the proximity of overall population density to habitat carrying capacity (*K*). Habituated bears tend to disproportionally use habitats near humans, especially in populations at or near *K* (Mattson, 1990; Mattson and others, 1992; Mattson and others, 1996). By contrast, wary bears disproportionally use habitats far away from humans. Thus, if habituated and wary bears are present in numbers proportional to the relative extent of areas influenced and uninfluenced by humans, no relative underuse of habitat near human facilities may be evident. By contrast, if a population is composed solely of wary bears, there may be virtually no use of human-influenced habitats. Habitat effectiveness, insofar as it varies with humans and their facilities, is largely an artifact of the relative numbers of habituated bears in any given population.

Relative numbers of habituated and wary bears in a population are predictably an artifact of the relative rates at which they die and are recruited (Pease and Mattson, 1999). Given that humans are almost always the cause of death for adult grizzly bears (Mattson and others, 1996), and given that reproductive rate varies little between habituated and wary females in places like the Yellowstone ecosystem (Pease and Mattson, 1999), relative numbers of habituated and wary bears are determined largely by differences in the rate at which they are killed by humans. In most places, habituated bears are likely killed at a greater rate (see Meagher and Fowler, 1989). In the Yellowstone ecosystem, this differential is twofold (Pease and Mattson, 1999). Thus, population-level underuse of habitat in the Yellowstone ecosystem near human facilities (Mattson and others, 1987) is likely a consequence of humans killing habituated bears at a greater rate than wary bears (Mattson and others, 1996; Pease and Mattson, 1999), together with normal avoidance of human facilities by the relatively more numerous wary individuals. By contrast, because grizzly bears exhibit such a high degree of behavioral plasticity (Herrero, 1985, 1989; Gilbert, 1989), it is highly unlikely that such underuse is a consequence of some fundamental inability of grizzly bears to tolerate humans (Mattson and others, 1996).

Because grizzly bears apparently avoid humans and human facilities with their avoidance contingent on behavioral characteristics of the bear population (which is, in turn, contingent on relative rates of human-caused mortality), the application of research to management is complicated. Avoidance of human facilities is typically expressed as relative underuse of habitat that varies with distance. Because bears have rarely been differentiated by their tolerance of humans, research results strongly reflect historical patterns of human-caused mortality. Judging the effects of human facilities on grizzly bears from this kind of research presupposes that (1) the same relative mix of habituated and wary bears is desired for the future and (2) wary and adult bears will continue to be killed by humans at the same rates as before. However, it may be that managers want to judge the impacts by humans, assuming that humans are much more tolerant of habituated animals. If it were assumed that humans were highly tolerant, simple representations of habitat productivity could be sufficient for judging the impacts of management. More likely, decisionmakers will want to judge the impacts of humans on wary bears since these animals have behavioral and demographic characteristics that are more desirable than those of habituated bears. In either case, research results that pool behavioral types deprive decisionmakers of relevant information.

The effects of humans or human facilities on use of habitats and foods by grizzly bears have been investigated in three primary ways. Most commonly, such effects have been inferred from spatial patterns of telemetry locations of radio-marked bears. Less often, effects have been inferred from direct observation of bears or the observation of durable signs. Each approach has its strengths and weaknesses. Telemetry locations have the advantage of potentially being classified according to the type of bear, whether on the basis of behavior, gender, age, or reproductive status. At the same time, telemetry locations are potentially subject to several biases. As evident in this study, there is a tendency to oversample bears that live near roads, especially in large study areas with few roads and prohibitions on low-level helicopter activity in wilderness areas. Trapping may modify the behavior of bears and interject additional bias in subsequent observations of captured animals (Gilbert, 1989). There is also a strong bias towards locating animals during daylight hours, with the possibility that nighttime use of areas near humans goes undetected (Olson and others, 1998). Radio-telemetry locations also do not reveal anything about the associated activity of the bear, that is, a bear could be near humans but engaging in much less efficient foraging behavior compared to when it is in the back country (Mattson and others, 1987). Direct observation provides much valuable information about the details of human-grizzly bear interactions and the potential to differentiate behaviors of individual bears (e.g., Warner, 1987; Fagan and Fagan, 1994; Olson and Gilbert, 1994; Olson and others, 1997, 1998). On the other hand, direct observation is typically restricted to daylight hours and areas with good visibility. The geographic scope of research is also typically limited. Observation of durable signs has several advantages. It can focus on use of specific high-quality foods, provided that use of these foods is easily detected. Activity not related to the consumption of important foods is also implicitly censored. Such an approach is additionally not subject to biases interjected by the daily activity patterns of researchers. Among the disadvantages of observing durable signs, activity by different bear species is not readily differentiated and signs cannot be easily classified according to different types of bears. In short, the strengths and weaknesses of these different research tools require that scientists and managers be discriminating in their applications and judicious with their interpretations.

Section 2.2: Approach

For purposes of the Yellowstone grizzly bear cumulative effects model (CEM), we defined "effective habitat productivity" as that part of the net digested energy potentially derived from an area available to bears according to their response to humans or human facilities. We calculated effective habitat productivity as the product of "habitat productivity" (described previously) times "coefficients of habitat effectiveness" (he_{jp}), applied contingent on a location being within a "zone-of-influence" (zoi_{jp}); he_{jp} and zoi_{jp} were specific to a given season (j) and type of human activity or facility (p). Coefficients of habitat effectiveness were, in theory, proportional to the fraction of potential net digested energy that was extracted by bears within a zone-of-influence (ZOI).

We categorized human activities and facilities according to a generalized scheme described by Weaver and others (1986). Activities were first classed as motorized or nonmotorized. Features were then classed as linear, point, or dispersed. Levels of activity were categorized as low or high and as diurnal or 24-hour. Habitat adjacent to human-related features was further classified as "no-cover" or "high-cover." Major facilities, such as recreational developments or towns (for definition see "Density of Feeding Activity" under "Analysis Methods," p. 5 of the main body of the report), were placed in a category of their own.

We used research regarding the influences of humans and human facilities on grizzly bear behavior to define coefficients of habitat effectiveness (HE) and ZOIs for each of the generalized human features. This application of research results required that we translate conventionally identified features and activities such as roads, trails, campgrounds, and recreational developments into the more functional types used in the Yellowstone grizzly bear CEM. Where there were substantial differences in research results, we used a qualitative rule set for selecting which results to use. We gave first priority to results from the Yellowstone ecosystem. Among those studies, we gave priority to results obtained from the observation of durable signs. As indicated above, this type of data was less affected by some significant biases that otherwise compromised radio-telemetry data. Observation of durable signs was also more directly relevant to estimating the amount of energy obtained by bears, as signified by use of high-quality foods such as ungulates (Green and others, 1997), whitebark pine seeds (Mattson and Reinhart, 1997), and cutthroat trout spawning streams (Reinhart and Mattson, 1990). Finally, we gave priority to results that represented the probable responses of wary animals.

The behavior of wary bears is potentially of great interest to grizzly bear managers in the Yellowstone ecosystem. These bears have the highest survival rates (Mattson and others, 1992; Pease and Mattson, 1999) and are less of a threat to humans, primarily because they are less often in contact with humans (Herrero, 1985, 1989; Herrero and Fleck, 1990). Where possible, we selected coefficients from the available research results that represented the behavior of wary bears. In almost all cases, our judgement as to whether the results pertained to wary bears or not required that we interpret the study design and study area conditions. In areas with a history of grizzly bear hunting and at least moderate levels of human-caused mortality, or in areas with a recent episode of substantial grizzly bear mortality that was selective against known food-conditioned or human-habituated animals, we assumed that the majority of bears were wary.

In several instances, we were not able to interpret research results in terms that directly related to HE or ZOIs. In other cases, we could not find research results germane to a specific human feature. Under these circumstances, we used subjective judgement to assign HE and ZOI values, based primarily on effects ascribed to the next most similar human activity or facility. When the Yellowstone grizzly bear CEM was first developed in 1984, many coefficients were the result of subjective judgement by those involved (Weaver and others, 1986; Dixon, 1997). Subsequently, values have been revised twice, in 1994 and in this publication, to reflect recent research. As a result, most HE coefficients and ZOIs currently have some empirical basis.

Even the most recent research does not provide much detailed information on differences in grizzly bear responses to humans when in the open (no-cover) compared to when in cover (high-cover). Even so, there are strong indications that responses are more extreme when encounters occur in the open (Schleyer and others, 1984; Haroldson and Mattson, 1985; McLellan and Shackleton, 1989). In the absence of results concerning cover/noncover responses by grizzly bears to specific human features, we quantified the judgement of those who had estimated HE in 1984 for more systematic applications to subsequently revised coefficients. This quantification took the form of predicting absolute differences in HE between the mean and cover and noncover values for each category of human activity or facilities; the mean was typically the value with greatest empirical support. This relationship took the form of a polynomial and approached 0 at high (→ 1) and low (→ 0) values of HE (fig. 2-1).

Section 2.3: Coefficients of Habitat Effectiveness

Coefficients of habitat effectiveness (HE) and zones-of-influence (ZOIs) for human features in the Yellowstone grizzly bear CEM were quite variable (table 2-1). At one extreme, HE was reduced to about 10% within 5 km of major human facilities such as towns and sizable recreational developments. This level of reduction was based on three studies of durable sign and was interpreted primarily to reflect the behavior of wary bears (Reinhart and Mattson, 1990; Green and others, 1997; Mattson and Reinhart, 1997). At the other extreme, low levels of dispersed nonmotorized human activity were assumed to have virtually no average effect (98% HE) on the feeding behavior and habitat use of bears, accounting for the fact that infrequent and unpredictable back-country encounters with humans resulted in only short-term responses by bears (Jope and Shelby, 1984; Jope, 1985; Schleyer and others, 1984; Haroldson and Mattson, 1985; Wilker and Barnes, 1998). This latter effect, as well as all others related to dispersed human activity, was based on professional judgement shaped by the results of many studies of interactions between humans and bears in the back country, including interactions off-trail (e.g., Chester, 1980; Schleyer and others, 1984; Haroldson and Mattson, 1985; McLellan and Shackleton, 1989; Gunther, 1990; Albert and Bowyer, 1991; Revenko, 1994). Compared to the responses of bears to major human facilities, at one extreme, and dispersed back-country human activity, at the other extreme, all other human features had intermediate effects on bear behavior that were as much dependent on the extent of the ZOI as on the value of HE. For example,

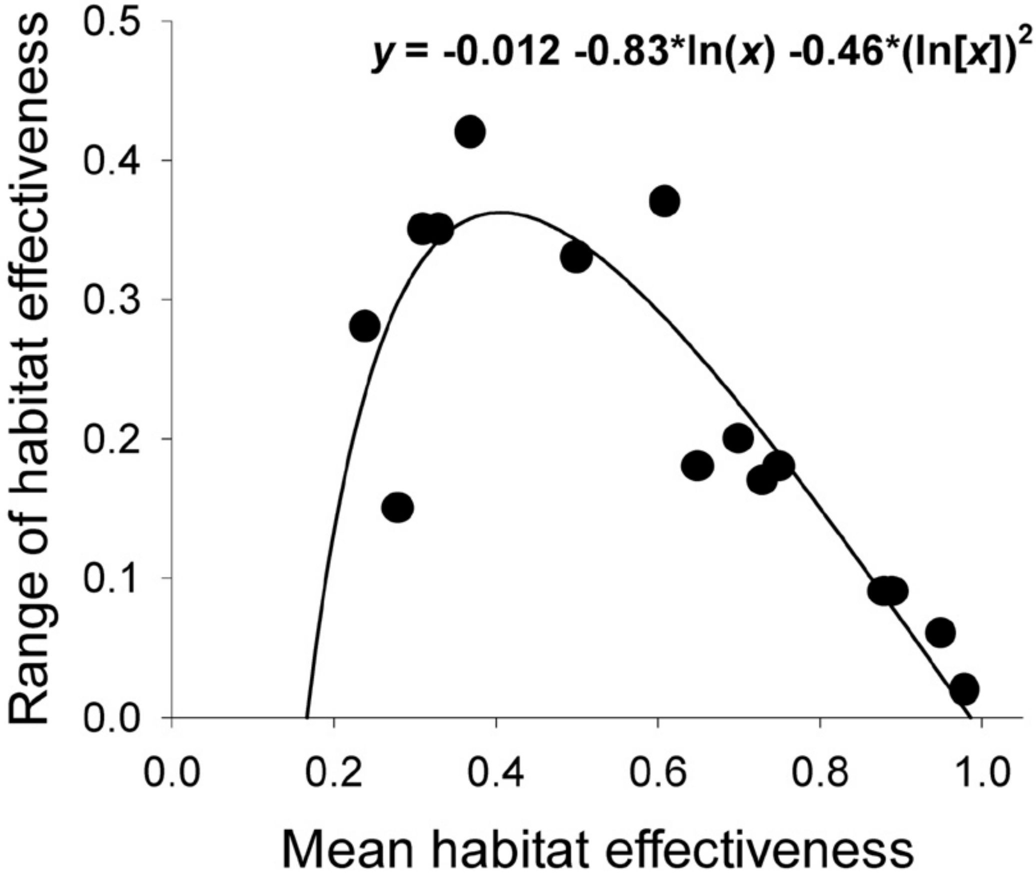

Figure 2-1. Relationship between the difference in value between cover and noncover for coefficients of habitat effectiveness (HE; range of habitat effectiveness) and the mean of these two values. Data are from original values assigned in 1984 and 1994 on the basis of professional judgement.

Table 2-1. Coefficients of habitat effectiveness and the associated extent of the zone-of-influence for human features in the Yellowstone grizzly bear cumulative effects model.

Category	Coefficient of habitat effectiveness			Zone-of-influence	References
	Mean	(Noncover /cover)	References		
Aircraft	0.61	(0.42/0.79)	Harding and Nagy, 1980; McLellan and Shackleton, 1988; Wilker and Barnes, 1998	mapped polygons	
Major development	0.08	(0.08/0.08)	Green and others, 1997; Mattson and Reinhart, 1997; Reinhart and Mattson, 1990	5000 m	Green and others, 1997; Mattson and Reinhart, 1997; Mattson and others, 1987, 1992
Linear motorized/high use	0.33	(0.21/0.45)	Green and others, 1997; Mattson and Reinhart, 1997	500 m	Gilbert, 1989; Mattson and Reinhart, 1997; Mattson and others, 1987
Linear motorized/low use	0.20	(0.19/0.21)	Archibald and others, 1987; Kasworm and Manley, 1990; McLellan and Shackleton, 1988	300 m	Archibald and others, 1987; Aune, 1994; Kasworm and Manley, 1990
Linear motorized/incidental	0.40[a]	(0.27/0.53)		300 m	
Motorized point diurnal/high use	0.28[b]	(0.18/0.38)		1000 m	
Motorized point diurnal/low use	0.57	(0.47/0.67)	Gunther, 1990	1000 m	Harding and Nagy, 1980
Motorized point/24-hr	0.28[b]	(0.18/0.38)		1000 m	
Motorized dipsersed/high use	0.31	(0.13/0.48)		mapped polygons	
Motorized dispersed/low use	0.75	(0.66/0.84)		mapped polygons	
Nonmotorized linear/high use	0.25[c]	(0.18/0.32)		300 m	
Nonmotorized linear/low use	0.51	(0.39/0.62)	Kasworm and Manley, 1990	300 m	Kasworm and Manley, 1990
Nonmotorized point/diurnal	0.57	(0.47/0.67)	Gunther, 1990	500 m	Gunther, 1990
Nonmotorized point/24-hr	0.28[b]	(0.18/0.38)		500 m	
Nonmotorized dispersed/high use	0.95	(0.92/0.98)		mapped polygons	
Nonmotorized dipsersed/low use	0.98	(0.97/0.99)		mapped polygons	

[a] This value is twice that of the "linear motorized/low use."

[b] This value is one-half that of "motorized point diurnal/low use."

[c] This value is one-half that of "nonmotorized linear/low use."

although HE for little-used roads was less than that of heavily used roads, the corresponding ZOI was only two-thirds as extensive. Thus, the overall effect of a major road was less per unit area but more widespread. Similarly, the effects of motorized point activities were distinguished from those of nonmotorized point activities by a ZOI that encompassed a geometrically larger area. In general, varying both HE and the ZOI allowed for greater sensitivity to the behavior of bears as reflected in diverse research results.

Section 2.4: Discussion

As discussed earlier, at the scale of population-level movements grizzly bears underuse habitats near humans largely to the extent that human-caused mortality has been selective against habituated animals. In other words, population-level patterns predictably are determined by the relative numbers of habituated and wary animals, who typically select, respectively, for and against areas near humans. Population-level patterns are thus an amalgam of effects attributable to selective human-caused mortality and the distinct behavioral characteristics of surviving individual bears.

It is important for management and research purposes to differentiate the effects of bear mortality and bear behavior as much as possible. Human-caused mortality is determined as much by human behavior as by bear behavior. Conversely, use of areas near humans by surviving bears is determined, at least proximally, by behavior of the bears alone. Bear behaviors and human-caused mortality entail different management issues and different related management decisions. Managing habituated bears and their death rate is intimately tied to managing humans. Moreover, managing human-caused mortality is almost wholly contingent on human values and world views that engender either tolerance or intolerance for grizzly bears that can live near us. Managing wary bears is a different class of problem. The preservation of wary bears largely depends on providing them with areas remote from humans where they can meet their energy needs without losing their fear of humans. The main concern is preventing habituation to humans and a doubled death rate. Thus, insofar as management of native habitat is concerned, it is the behavioral responses of wary bears that are germane. By contrast, the management of habituated bears largely entails the modification of human behavior and the management of bear attractants at human facilities.

The coefficients of habitat effectiveness presented here are, at best, a crude representation of the behavior of wary grizzly bears. However, the coefficients have merits. They constitute an effort to present information in a way that is maximally relevant to management deliberations both by emphasizing the behavior of wary bears and by being attentive to the many types of human activities that are present in grizzly bear habitat. By contrast, analyses of radio-telemetry data from the Yellowstone ecosystem to detect patterns of habitat use have, with one exception (Mattson and others, 1992), admixed habituated and wary animals and have not very well accounted for spatial sampling biases introduced either through trapping or radio-telemetry location efforts. Also, the available samples are not large enough in size to estimate the many parameters needed to control for spatial and temporal biases as well as the parameters that characterize responses of radio-marked bears to different types of human activities. Future analyses could exclusively focus on wary bears, but such parsing would only exacerbate problems with sample sizes.

Managers who rely on decision-support systems such as the Yellowstone grizzly bear CEM are thus confronted with the commonplace tension between a need for relevance and the limits of empiricism. Wholesale speculation is obviously undesirable because it entails substantial risk of leading to unintentionally harmful decisions. Hide-bound empiricism is also undesirable because, by default, all of the effects unable to be estimated, either because of deficient sample sizes or research designs, are typically assumed to be zero. Quite often, in the absence of statistical empiricism, management decisions are made based on undisclosed premises about the state of a system, without benefitting from well-developed qualitative scientific understanding. The overly empirical approach clearly also entails substantial risk. From the perspective of risk to the managed resource, some middle ground is optimal. In this analysis, we strove to find the middle ground between empiricism and informed speculation in developing coefficients of habitat effectiveness for the Yellowstone grizzly bear CEM.

Appendix 2 References

Albert, D.M., and Bowyer, R.T., 1991, Factors related to grizzly bear-human interactions in Denali National Park: Wildlife Society Bulletin, v. 19, p. 339-349.

Archibald, W.R., Ellis, R., and Hamilton, A.N., 1987, Responses of grizzly bears to logging truck traffic in the Kimsquit River Valley, British Columbia: International Conference on Bear Research and Management, v. 7, p. 251-257.

Aumiller, L.D., and Matt, C.A., 1994, Management of McNeil River State Game Sanctuary for viewing brown bears: International Conference on Bear Research and Management, v. 9, p. 51-61.

Aune, K.E., 1994, Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana: International Conference on Bear Research and Management, v. 9, p. 365-374.

Chester, J.M., 1980, Factors influencing human-grizzly bear interactions in a backcountry setting: International Conference on Bear Research and Management, v. 4, p. 351-357.

Dixon, B.G., 1997, Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem: Bozeman, Mont., Montana State University, M.S. thesis, 192 p.

Fagan, J.M., and Fagan, R., 1994, Interactions between wildlife viewers and habituated brown bears, 1987-1992: Natural Areas Journal, v. 14, p. 159-164.

Gilbert, B.K., 1989, Behavioural plasticity and bear-human conflicts, *in* Bromley, M., ed., Bear-people conflicts — proceedings of a symposium on management strategies: Yellowknife, Northwest Territories, Canada, Northwest Territories Department of Renewable Resources, p. 1-8.

Green, G.I., Mattson, D.J., and Peek, J.M., 1997, Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park: Journal of Wildlife Management, v. 61, p. 1040-1055.

Gunther, K.A., 1990, Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park: International Conference on Bear Research and Management, v. 8, p. 73-78.

Harding, L., and Nagy, J.A., 1980, Responses of grizzly bears to hydrocarbon exploration on Richards Island, Northwest Territories, Canada: International Conference on Bear Research and Management, v. 3, p. 277-280.

Haroldson, M., and Mattson, D.J., 1985, Response of grizzly bears to backcountry human use in Yellowstone National Park: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team Report, 38 p.

Herrero, S., 1985, Bear attacks: their causes and avoidance: Piscataway, N.J., Nick Lyons Books/Winchester Press, 287 p.

Herrero, S., 1989, The role of learning in some fatal grizzly bear attacks on people, *in* Bromley, M., ed., Bear-people conflicts — proceedings of a symposium on management strategies: Yellowknife, Northwest Territories, Canada, Northwest Territories Department of Renewable Resources, p. 9-14.

Herrero, S., and Fleck, S., 1990, Injury to people inflicted by black, grizzly or polar bears: recent trends and new insights: International Conference on Bear Research and Management, v. 8, p. 25-32.

Jope, K.L., 1985, Implications of grizzly bear habituation to hikers: Wildlife Society Bulletin, v. 13, p. 32-37.

Jope, K.L., and Shelby, B., 1984, Hiker behavior and the outcome of interactions with grizzly bears: Leisure Science, v. 6, p. 257-270.

Kasworm, W.F., and Manley, T.L., 1990, Road and trail influences on grizzly bears and black bears in northwest Montana: International Conference on Bear Research and Management, v. 8, p. 79-84.

Mattson, D.J., 1990, Human impacts on bear habitat use: International Conference on Bear Research and Management, v. 8, p. 33-56.

Mattson, D.J., Blanchard, B.M., and Knight, R.R., 1992, Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops: Journal of Wildlife Management, v. 56, p. 432-442.

Mattson, D.J., Herrero, S., Wright, R.G., and Pease, C.M., 1996, Designing and managing protected areas for grizzly bears: how much is enough?, *in* Wright, R.G., ed., National Parks and protected areas: their role in environmental protection: Cambridge, Mass., Blackwell Science, p. 133-164.

Mattson, D.J., Knight, R.R., and Blanchard, B.M., 1987, The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming: International Conference on Bear Research and Management, v. 7, p. 259-273.

Mattson, D.J., and Reinhart, D.P., 1997, Excavation of red squirrel middens by Yellowstone grizzly bears: Journal of Applied Ecology, v. 34, p. 926-940.

McLellan, B.N., and Shackleton, D.M., 1988, Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography: Journal of Applied Ecology, v. 25, p. 451-460.

McLellan, B.N., and Shackleton, D.M., 1989, Immediate reactions of grizzly bears to human activities: Wildlife Society Bulletin, v. 17, p. 269-274.

Meagher, M., and Fowler, S., 1989, The consequences of protecting problem grizzly bears, *in* Bromley, M., ed., Bear-people conflicts — proceedings of a symposium on management strategies: Yellowknife, Northwest Territories, Canada, Northwest Territories Department of Renewable Resources, p. 141-144.

Olson, T.L., and Gilbert, B.K., 1994, Variable impacts of people on brown bear use of an Alaskan river: International Conference on Bear Research and Management, v. 9, p. 97-106.

Olson, T.L., Gilbert, B.K., and Squibb, R.C., 1997, The effects of increasing human activity on brown bear use of an Alaskan river: Biological Conservation, v. 82, p. 95-99.

Olson, T.L., Squibb, R.C., and Gilbert, B.K., 1998, Brown bear diurnal activity and human use: a comparison of two salmon streams: Ursus, v. 10, p. 547-555.

Pease, C.M., and Mattson, D.J., 1999, Demography of the Yellowstone grizzly bears: Ecology, v. 80, p. 957-975.

Reinhart, D.P., and Mattson, D.J., 1990, Bear use of cutthroat trout spawning streams in Yellowstone National Park: International Conference on Bear Research and Management, v. 8, p. 343-350.

Revenko, I.A., 1994, Brown bear (*Ursus arctos piscator*) reaction to humans on Kamchatka: International Conference on Bear Research and Management, v. 9, p. 107-108.

Schleyer, B., Jonkel, J., Rhoades, K., and Dunbar, D., 1984, The effects of nonmotorized recreation on grizzly bear behavior and habitat use: Bozeman, Mont., National Park Service, Interagency Grizzly Bear Study Team Report, 83 p.

Warner, S.H., 1987, Visitor impact on brown bears, Admiralty Island, Alaska: International Conference on Bear Research and Management, v. 7, p. 377-382.

Weaver, J., Escano, R., Mattson, D., and Puchlerz, T., 1986, Cumulative effects process for the Yellowstone ecosystem, *in* Contreras, G., and Evans, K., compilers, Proceedings — grizzly bear habitat symposium: U.S. Forest Service General Technical Report INT-207, p. 234-246.

Wilker, G.A., and Barnes, V.G., Jr., 1998, Responses by brown bears to human activities at O’Malley River, Kodiak Island, Alaska: Ursus, v. 10, p. 557-561.

Appendix 3. Habitat Types and Corresponding Codes Used in the Yellowstone Grizzly Bear Cumulative Effects Model

Habitat	New codes	Previously mapped codes
Nonforest types		
Clover patches	00001	Not mapped[1]
Dry meadows and grasslands	00002	00013, 00024, 00035, 000074
High-water-table flux wetlands	00003	Not mapped[1]
Lithic ridges	00004	00015, 00034, 00051
Marshes and fens	00005	00021, 00031, 00071
Mesic meadows and grasslands	00006	00012, 00023, 00033, 00042, 00057, 00058, 00073
Talus and scree	00007	0053
Wet meadows	00008	00011, 00014, 00022, 00032, 00041, 00072, 00081, 00082
Miscellaneous other existing nonforest codes	00009	00052, 00054, 00055, 00056, 00059, 00060, 88808, 99909; these will be assigned coefficients of 0. Code 66606 (agricultural lands) will be retained and assigned a coefficient pending further discussion.
Forest types		
Dry forest openings created by timber harvest or fire	10100	All "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) of types designated by the new codes as: 10101, 10201, 10301, 10401, or 10501, respectively.
High elevation subalpine fir climax sites	10101	All cover types except "0" cover (__10, __20, __30, __40, __50, __60, __70, __80) and except whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 461, 462, 475, 493, 497, 670, 671, 690, 701, 707, 710, 711, 745, 770, 780, 781, 782, 783, 784, 810, 811, 830, 840, or 842.
High elevation whitebark pine-dominated sites	10201	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) of the following habitat types (old codes): 734, 812, 820, 821, 825, 850, 870, 875, 880, 881, 885, 887, 891, 895, or 897; plus all whitebark pine cover types (__51, __52, __53, __54, __63), excluding __50, associated with any other habitat type.
High elevation or dry Douglas-fir-dominated sites	10301	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) and whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 040, 050, 051, 060, 070, 080, 092, 093, 095, 210, 212, 220, 221, 311, 321, 330, 360, 370, 371, 372, 373, 380, 385, 395, 396, 397, 398, 399, 495, 702, 703, or 704.
Sites dominated by grouse whortleberry	10401	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) and whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 460, 485, 640, 663, 692, 721, 730, 731, 732, 733, 735, 831, 920, or 940.
Low elevation lodgepole pine-dominated sites	10501	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) and whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 790, 791, 792, 795, 896, 901, 902, 903, 910, 935, 945, 950, 955, 956, 965, or 970.
Low elevation spruce-dominated sites	10601	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) and whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 410, 421, 440, 470, 480, 490, 660, 661 or 911.
Mesic subalpine fir climax sites	10701	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) and whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 415, 601, 609, 610, 620, 621, 623, 630, 635, 636, 650, 651, 653, 654, 740, 750, 751, 752, 760, 761, 762.
Mesic forest openings created by timber harvest or fire	10600	All "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) of types designated by the new codes as: 10601, 10701, or 10801, respectively.
Mesic Douglas-fir-dominated sites	10801	All cover types except "0" cover types (__10, __20, __30, __40, __50, __60, __70, __80) and whitebark pine-dominated cover types (__51, __52, __53, __54, __63) of the following habitat types (old codes): 260, 261, 262, 280, 281, 290, 291, 292, 293, 310, 312, 313, 320, 322, 323, 325, 340, 341, 343, 375, 390, 391, 430, 432, 603, 607, 645, 647, 691, 705, 720, 722, 723, 724, or 990.

[1] These habitat components are identified and mapped based on site-specific knowledge.

Appendix 4. Relative Net Energy (kilocalories) Digested per Gram of Food Ingested by Yellowstone Grizzly Bears

Food or Activity	Season	Digested kilocalories per gram	(ee_{ij}) Expended energy per gram (index)	($nete_{ij}$) Net energy per gram (index)
Ungulates				
Wapiti calves	estrus	4.23	0.34	3.99
Adult wapiti	spring	4.10	0.21	3.99
Adult wapiti	estrus	4.10	0.42	3.78
Adult wapiti	early hyperphagia	5.17	0.34	4.93
Adult wapiti	late hyperphagia	6.08	0.34	5.84
Bison	spring	4.29	0.28	4.11
Bison	estrus	4.29	0.28	4.11
Bison	early hyperphagia	4.85	0.25	4.70
Bison	late hyperphagia	5.49	0.25	5.34
Moose	spring	4.29	0.28	4.11
Moose	estrus	4.29	0.28	4.11
Moose	early hyperphagia	4.85	0.34	4.61
Moose	late hyperphagia	5.49	0.34	5.25
Hymenoptera				
In logs	year-round	3.25	3.25	0.10
In hills	year-round	3.25	0.31	3.04
Under logs	year-round	3.25	1.76	1.59
Under rocks	year-round	3.25	2.35	1.00
Under dung	year-round	3.25	1.50	1.85
Hornets	year-round	2.74	2.67	0.17
Excavated animals and caches				
Pocket gophers	spring	1.98	0.24	1.84
Pocket gophers	estrus	2.08	0.23	1.95
Pocket gophers	early hyperphagia	2.66	0.86	1.90
Pocket gophers	late hyperphagia	2.55	0.94	1.71
Voles	spring	3.27	0.87	2.50
Voles	estrus	3.27	0.47	2.90
Voles	early hyperphagia	3.27	2.30	1.07
Voles	late hyperphagia	1.88	0.12	1.86
Worms	year-round	3.19	1.14	2.15
Whitebark pine	early hyperphagia	2.73	0.37	2.46
Whitebark pine	late hyperphagia	2.73	0.28	2.55
Mushrooms	year-round	1.67	0.02	1.75
Huckleberry	year-round	2.74	0.03	2.81
Whortleberry	year-round	2.70	0.11	2.69
Buffaloberry	year-round	2.75	0.05	2.80
Strawberry	year-round	2.71	0.06	2.75
Roots				
Yampa	spring	2.85	0.50	2.45
Yampa	estrus	2.82	0.19	2.73
Yampa	early hyperphagia	2.82	0.43	2.49
Yampa	late hyperphagia	2.82	0.55	2.37
Biscuitroot	spring	2.44	0.18	2.36
Biscuitroot	estrus	2.41	0.18	2.33
Biscuitroot	early hyperphagia	2.36	0.30	2.16
Biscuitroot	late hyperphagia	2.36	0.30	2.16
Sweet-cicely	year-round	2.47	0.33	2.24
Pondweed	year-round	2.13	0.31	1.92

Appendix 4. —Continued.

Food or Activity	Season	Digested kilocalories per gram	(ee_{ij}) Expended energy per gram (index)	($nete_{ij}$) Net energy per gram (index)
Grazed foods				
Graminoids	spring	1.29	0.12	1.27
Graminoids	estrus	1.21	0.08	1.23
Graminoids	early hyperphagia	0.68	0.06	0.72
Graminoids	late hyperphagia	0.68	0.06	0.72
Clover	spring	2.01	0.08	2.03
Clover	estrus	1.53	0.08	1.55
Clover	early hyperphagia	1.47	0.04	1.53
Clover	late hyperphagia	1.47	0.04	1.53
Dandelion	year-round	1.64	0.05	1.69
Thistle	year-round	0.67	0.03	0.74
Fireweed	spring	1.69	0.06	1.73
Fireweed	estrus	1.69	0.06	1.73
Fireweed	early hyperphagia	2.18	0.06	2.22
Fireweed	late hyperphagia	2.18	0.06	2.22
Horsetail	year-round	1.06	0.03	1.13
Spring beauty	year-round	1.77	0.17	1.70

Appendix 5. Conversion Factors ($cfctr_{ij}$) from Units of Activity Measured at Grizzly Bear Feeding Sites to Relative Grams of Food Obtained by Bears

[Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

Food or Activity	Season			
	Spring	Estrus	Early hyperphagia	Late hyperphagia
Ungulates				
Ungulate meat (g/kg)	6.51	17.44	14.17	4.68
Hymenoptera				
Ants_logs (g/dm^3)	0.11	0.17	0.24	0.93
Ants_hills (g/dm^3)	1.57	1.59	0.40	0.40
Ants_under logs (g/dm^3)	0.05	0.08	0.12	0.46
Ants_under rocks (g/rock)	0.05	0.08	0.12	0.46
Ants_under dung (g/feces)		0.08	0.12	
Hornets (g/dm^3)		0.75	0.75	0.75
Excavated animals and caches				
Pocket gophers (g/dm^3)	0.01	0.02	0.49	1.28
Worms (g/dm^3)	0.01	0.02		
Voles (g/dm^3)	0.01	0.02	0.49	1.28
Fruits, sporophytes, and seeds				
Whitebark pine (g/m^2)	26.18	13.09	5.04	25.16
Mushrooms (g/dig)		1.77	2.32	1.77
Huckleberry (g/feces)		2.00	38.80	30.50
Whortleberry (g/feces)		2.00	38.80	30.50
Buffaloberry (g/feces)			17.56	
Strawberry (g/feces)			48.00	
Other berries (g/feces)			20.80	20.80
Roots				
Yampa (g/dig)	0.52	0.52	0.18	4.00
Biscuitroot (g/dig)	0.03	0.03	0.07	0.07
Sweet-cicely (g/dig)			1.60	1.60
Pondweed (g/dm^3)	0.01	0.01	0.01	0.01
Grazed foods				
Graminoids (g/feces)	9.44	20.19	52.24	24.99
Clover (g/feces)	1.79	10.32	18.41	18.41
Dandelion (g/feces)	22.90	22.90	18.48	18.48
Thistle (g/stem)		10.06	10.06	
Fireweed (g/feces)	15.70	42.86	76.02	76.02
Horsetail (g/feces)	4.32	4.32	12.77	
Spring beauty (g/feces)	3.48	4.11		

Appendix 6. Mean Level of Feeding Activity by Grizzly Bears for Different Foods ($fslv_{ijk}$), in Food-specific Units

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T.	Spring					Estrus				Early hyperphagia					Late hyperphagia				
Code	Misc. Ung.	Wapiti calf	Wapiti adult	Bison	Moose	Wapiti calf	Wapiti adult	Bison	Moose	Misc. Ung.	Wapiti calf	Wapiti adult	Bison	Moose	Misc. Ung.	Wapiti calf	Wapiti adult	Bison	Moose
Ungulates = “ung.” (kilograms dry weight)																			
2		12	23	90		2	31	124	34			37	134						
4			28				39												
6			22	91		3	36	94				68	146					141	
8		29	69	100	39	3	39	92			3	48	163				89	146	
10100						14						23	149		1	2	14		
10101					35														
10201			20			3													
10301	1		38				43												
10401				130		3		118	65			66	158	114			30	170	114
10501		29	39	80		3	34	115				76					65	85	
10600			9			3	35					60							
10601				32	52	3					10	72		90					
10701		23	20	254	51	3	33	159	41			29			4		54	36	154
10801	3	38	20							3									
Mean	2	26	29	111	44	4	36	117	47	3	7	53	150	102	3	2	50	116	134

Mean level of feeding activity by grizzly bears for different foods ($fslv_{ijk}$), in food-specific units.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T. Code	**Spring**			**Estrus**				**Early hyperphagia**				**Late hyperphagia**		
	Grass	**Clover**	**Dandelion**	**Grass**	**Clover**	**Dandelion**	**Thistle**	**Grass**	**Clover**	**Dandelion**	**Thistle**	**Grass**	**Clover**	**Dandelion**
Grazed foods (grasses and sedges [grass], clover, and dandelion [number of feces]; thistle [number of stems])														
2	2.9	5.1	2.0	2.1	1.8	2.2	14.0	1.8	7.0		12.0	1.7		
4	1.5			1.0	1.0	1.0		2.0	4.4		13.0			
6	1.7	2.5	3.0	2.5	2.0	1.6	13.0	3.6	1.0	3.2	9.0	1.5		
8	5.8	10.2	6.0	4.4	4.3	1.7	16.0	6.5	10.0	1.5	6.0	2.6	9.0	2.0
10100	2.3		2.0	2.0	16.0	1.0	1.0	4.0					2.0	3.0
10101				1.7	2.0							2.0		
10201	2.0							3.3				2.0		
10301				1.0		1.0								
10401	1.0			3.0								1.0		
10501	1.0			2.0				5.0						
10600	1.7	2.0	1.0	1.9	1.5	2.8	2.0	3.5	8.9	1.3	1.0		1.0	
10601				2.0		3.0		7.2	1.0	1.0				
10701	2.2		1.0	2.1	1.5	1.4	2.0	1.2	1.5	1.8	7.0	1.2	15.0	1.0
10801	2.7			2.2	2.0	2.0		2.0				5.0	2.0	
Mean	2.3	5.0	2.5	2.1	3.6	1.8	8.0	3.6	4.8	1.8	7.7	2.1	5.8	2.0

Mean level of feeding activity by grizzly bears for different foods ($fslv_{ijk}$), in food-specific units.—Continued.

["H.T. Code" refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T. Code	Spring		Estrus		Early hyperphagia		Late hyperphagia	
	Logs	Hills	Logs	Hills	Logs	Hills	Logs	Hills
Ants in logs and hills (decimeter^3 excavated)								
2	181	5	32	37	805	28	59	28
4			1				60	
6	123	14	49	18	92	76	17	6
8	78	36	86	7	14	8	555	54
10100			22	3	48	1	131	
10101			129		68	19	34	
10201	114		111		62		63	
10301	5		238	17	208		81	
10401	89		85		89		56	
10501	49	1	50	1	110	19	43	
10600		21	55		111		54	
10601	51		108		363	34		
10701	36		111	8	108	139	83	
10801	178	217	96	47	111	6	73	
Mean	90	49	84	17	168	37	101	29

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
Other invertebrates				
Ants under rocks (decimeter^3)	239	90	101	46
Ants under logs (n)	68	55	60	16
Ants under dung (n)		21		
Hornets (decimeter^3)		28	48	28

Mean level of feeding activity by grizzly bears for different foods ($fslv_{ijk}$), in food-specific units.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T. Code	Spring	Estrus	Early hyperphagia	Late hyperphagia
Excavated root caches and animal foods: Pocket gophers (decimeter^3 excavated)				
2	213	1704	65	3
4		180	38	
6	412	475	110	116
8	440	198	152	
10100		36		
10101				
10201		12		
10301				
10401		28		
10501		1109		
10600		370	60	
10601				
10701	2	10		468
10801	13			70
Mean	216	412	85	164

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
Excavated root caches and animal foods: Other (decimeter^3 excavated)				
Worms	2153	15247		
Voles	38	99	99	121

Mean level of feeding activity by grizzly bears for different foods ($fslv_{ijk}$), in food-specific units.—Continued.

["H.T. Code" refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T. Code	Spring		Estrus		Early hyperphagia		Late hyperphagia	
	Seeds	Mushrooms	Seeds	Mushrooms	Seeds	Mushrooms	Seeds	Mushrooms
Whitebark pine seeds from middens and mushrooms (seeds = meter^2 excavated; mushrooms = number of digs)								
2								
4								
6								
8								
10100								
10101			43		28		24	21
10201	7		31		53	2	77	34
10301					20			
10401			28		22	6	25	18
10501			8	6	9	55	25	26
10600								
10601								
10701			27		27	96	37	5
10801					24	10	14	
Mean	7		27	6	26	34	34	21

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
Fruits (number of feces)				
Huckleberry			1.4	1.0
Whortleberry		3.0	1.2	1.0
Buffaloberry			3.7	3.7
Strawberry			1.7	
Other berries			4.7	1.5

Mean level of feeding activity by grizzly bears for different foods ($fslv_{ijk}$), in food-specific units.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T. Code	Spring		Estrus		Early hyperphagia		Late hyperphagia	
	Yampa	Biscuitroot	Yampa	Biscuitroot	Yampa	Biscuitroot	Yampa	Biscuitroot
				Yampa and biscuitroot (number of digs)				
2	12	82	11	457	339	161	40	80
4		516	115	304	36	514	12	315
6	9	455	116	28	366	78	71	
8			50		262		75	
10100		2	170	144	413	97		
10101								
10201		48		4		1		31
10301						100		
10401		2	8					
10501	3		1			3		
10600			27		14			
10601				61				
10701					19		14	
10801	5							
Mean	7	184	62	166	207	136	42	142

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
		Other roots		
Sweet-cicely (n)			26	65
Pondweed (decimeter^3)		15096		34056

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
		Other grazed foods (number of feces)		
Fireweed	1.0	1.3	2.2	3.0
Horsetail	2.6	2.6	2.6	
Spring beauty	2.0	2.4		

Appendix 7. Mean Index of Net Energy per Feeding Site ($fsne_{ijk}$) for Consumption of Different Foods by Grizzly Bears

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

	Spring					Estrus				Early hyperphagia					Late hyperphagia				
H.T. Code	Misc. ung.	Wapiti calf	Wapiti adult	Bison	Moose	Wapiti calf	Wapiti adult	Bison	Moose	Misc. ung.	Wapiti calf	Wapiti adult	Bison	Moose	Misc. ung.	Wapiti calf	Wapiti adult	Bison	Moose
Ungulates = “ung.”																			
2		301	596	2414		139	2040	8917	2408			2606	8951						
4			728				2584												
6			567	2447		230	2386	6764				4750	9703					3530	
8		752	1784	2685	1050	202	2564	6567			153	3367	10856				2424	3653	
10100						995						1586	9897		23	49	394		
10101					929														
10201			520			195													
10301	21		988				2821												
10401				3470		176		8458	4688			4639	10496	7473			829	4248	2811
10501		754	1012	2155		202	2241	8272				5309					1789	2126	
10600			234			195	2307					4205							
10601				857	1392	174					560	5030		5879					
10701	65	598	519	6787	1355	188	2182	11404	2910			2019			108		1482	911	3788
10801		998	524							200									
Mean	29	681	747	2974	1182	270	2391	8397	3335	200	357	3723	9981	6676	66	49	1384	2894	3300

Mean index of net energy per feeding site ($fsne_{ijk}$) for consumption of different foods by grizzly bears.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T.	Spring			Estrus				Early hyperphagia				Late hyperphagia		
Code	Grass	Clover	Dandelion	Grass	Clover	Dandelion	Thistle	Grass	Clover	Dandelion	Thistle	Grass	Clover	Dandelion
Grazed foods (grasses and sedges [grass], clover, dandelion, and thistle)														
2	35	19	77	52	28	85	101	66	197		87	30		
4	18			25	16	39		75	124		93			
6	20	9	116	62	32	64	95	135	28	102	66	27		
8	69	37	232	110	69	67	119	245	282	94	41	47	254	63
10100	27		77	50	256	39	7	151					56	94
10101				41	32							36		
10201	24							125				36		
10301				25		39								
10401				75								18		
10501				50				188						
10600	21	7	39	47	24	107	15	132	251	40	7		28	
10601				50		116		273	28	31			423	
10701	27		39	53	24	55	15	45	42	56	48	23	56	31
10801	32			56	32	77		75				90	163	
Mean	30	18	97	53	51	69	59	137	136	65	57	38	163	62

Mean index of net energy per feeding site ($fsne_{ijk}$) for consumption of different foods by grizzly bears.—Continued.

["H.T. Code" refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T.	**Spring**		**Estrus**		**Early hyperphagia**		**Late hyperphagia**	
Code	**Logs**	**Hills**	**Logs**	**Hills**	**Logs**	**Hills**	**Logs**	**Hills**
				Ants in logs and hills				
2	1.9	24.8	0.5	177.8	19.5	33.5	5.4	34.7
4		0.0				5.5		
6	1.3	64.8	0.8	89.5	2.2	93.0	1.6	7.8
8	0.8	172.6	1.4	35.8	0.3	10.0	51.5	65.3
10100			0.4	12.1	1.2	1.0	12.1	
10101			2.2		1.6	22.6	3.1	
10201	1.2		1.9		1.5		5.9	
10301	0.1		4.0	80.3	5.0		7.5	
10401	1.0		1.4		2.2		5.2	
10501	0.5	5.7	0.8	4.8	2.7	23.4	4.0	
10600		100.6	0.9		2.7		5.0	
10601	0.5		1.8		8.8	41.4		
10701	0.4		1.9	38.7	2.6	169.0	7.7	
10801	1.9	1035.3	1.6	227.5	2.7	6.8	6.7	
Mean	1.0	234.0	1.4	83.3	4.1	44.5	9.3	35.9

Food source	**Spring**	**Estrus**	**Early hyperphagia**	**Late hyperphagia**
		Other invertebrates		
Ants under rocks	20.3	12.0	19.4	33.6
Ants under logs	3.6	4.7	7.2	7.4
Ants under dung		3.3	0.3	
Hornets		3.5	6.2	3.6

Mean index of net energy per feeding site (*fsne*$_{ijk}$) for consumption of different foods by grizzly bears.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T. Code	Spring	Estrus	Early hyperphagia	Late hyperphagia
Excavated root caches and animal foods: Pocket gophers				
2	4.6	65.4	60.6	6.3
4		6.9	34.9	
6	8.9	18.2	102.3	252.2
8	9.6	7.6	141.4	
10100		1.4		
10101				
10201		0.5		
10301				
10401		1.1		
10501		42.6		
10600		14.2	55.9	
10601				
10701	0.1	0.4		33.3
10801	0.2			151.8
Mean	4.7	15.8	79.0	110.9

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
Excavated root caches and animal foods: Other				
Worms	54.6	646.9		
Voles	1.1	5.7	51.7	287.9

Mean index of net energy per feeding site (*fsne*$_{ijk}$) for consumption of different foods by grizzly bears.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T.	Spring		Estrus		Early hyperphagia		Late hyperphagia	
Code	Seeds	Mushrooms	Seeds	Mushrooms	Seeds	Mushrooms	Seeds	Mushrooms
Whitebark pine seeds from middens and mushrooms								
2								
4								
6								
8								
10100								
10101			1468		351		1545	65
10201	454		1068		655	8	2759	104
10301					242			
10401			986		270	24	1610	57
10501			283	19	113	222	1626	80
10600								
10601								
10701			947		332	390	2355	15
10801					298	41	917	
Mean	454		950	19	323	137	1802	64

Food Source	Spring	Estrus	Early hyperphagia	Late hyperphagia
Fruits				
Huckleberry			153	86
Whortleberry		16	127	82
Buffaloberry			180	180
Strawberry			226	
Other berries			268	86

Mean index of net energy per feeding site (*fsne*$_{ijk}$) for consumption of different foods by grizzly bears.—Continued.

[“H.T. Code” refers to habitat type code. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

H.T.	**Spring**		**Estrus**		**Early hyperphagia**		**Late hyperphagia**	
Code	**Yampa**	**Biscuitroot**	**Yampa**	**Biscuitroot**	**Yampa**	**Biscuitroot**	**Yampa**	**Biscuitroot**
				Yampa and biscuitroot				
2	15.8	5.7	15.2	31.6	148.4	25.2	380.8	12.5
4		36.2	162.2	21.0	15.5	80.5	113.8	49.3
6	11.4	31.9	162.7	1.9	160.2	12.2	744.6	
8			70.0		114.8		711.4	
10100		0.1	239.1	10.0	180.5	15.2		
10101								
10201		3.4		0.3		0.2		4.9
10301						15.7		
10401		0.1	11.3					
10501	3.8		1.4			0.5		
10600			38.0		3.7			
10601				4.2				
10701					4.7		132.8	
10801	6.3							
Mean	9.3	12.9	87.5	11.5	89.7	21.4	416.7	22.2

Food Source	**Spring**	**Estrus**	**Early hyperphagia**	**Late hyperphagia**
		Other roots		
Sweet-cicely			92	233
Pondweed		339	552	765

Food source	**Spring**	**Estrus**	**Early hyperphagia**	**Late hyperphagia**
		Other grazed foods		
Fireweed	27	104	368	506
Horsetail	8	8	23	
Spring beauty	34	40		

Appendix 8. Proportion of Grizzly Bear Radio-relocations with Feeding Activity (p = $pact_{jkl}$)

[Sample sizes (*n*) are given. Years are distinguished by whether carrion was abundant or not (Ung = Y or N) and by whether whitebark pine seeds were abundant or not (Wbp = Y or N). "H.T. Code" refers to habitat type code]

H.T. Code	**Spring**				**Estrus**		**Early hyperphagia**				**Late hyperphagia**			
	Ung = Y		**Ung = N**				**Wbp = Y**		**Wbp = N**		**Wbp = Y**		**Wbp = N**	
	p	***n***	**p**	***n***	**p**	***n***	**p**	***n***	**p**	***n***	**p**	***n***	**p**	***n***
2	0.30	23	0.22	16	0.51	65	0.64	11	0.43	10	0.45	11	0.44	9
4	0.86	7	0.86	7	0.91	43	0.86	14	1.00	12	0.60	10	0.60	10
6	0.88	25	0.86	21	0.82	65	0.92	27	0.90	21	0.77	13	0.83	12
7	0.86	7	0.86	7	0.91	43	0.86	14	1.00	12	0.60	10	0.60	10
5 and 8	0.64	11	0.64	11	0.66	32	0.81	16	0.67	24	0.85	13	0.85	13
10100	0.59	22	0.56	18	0.29	63	0.21	14	0.25	24	0.25	8	0.36	11
10101	0.18	11	0.18	11	0.10	31	0.48	25	0.64	11	0.57	14	0.50	18
10201	0.27	11	0.27	11	0.35	74	0.54	57	0.48	23	0.73	113	0.67	15
10301	0.11	9	0.11	9	0.21	19	0.33	6	0.33	6	0.17	6	0.17	6
10401	0.22	9	0.11	18	0.23	116	0.33	27	0.41	22	0.41	34	0.58	19
10501	0.33	21	0.42	24	0.20	41	0.50	24	0.32	19	0.48	23	0.50	18
10600	0.72	18	0.69	13	0.42	71	0.42	33	0.67	24	0.40	5	0.40	5
10601	0.14	7	0.14	7	0.22	37	0.60	10	0.64	11	0.58	12	0.58	12
10701	0.36	14	0.21	19	0.35	125	0.44	64	0.52	33	0.53	30	0.59	37
10801	0.38	16	0.42	12	0.34	50	0.57	14	0.80	15	0.67	9	0.83	12

Appendix 9. Relative Density of Grizzly Bear Feeding Activity by Region, Habitat Type, Season, and Year Type

[Years are distinguished by whether carrion was abundant or not (Ung = Y or N) and by whether whitebark pine seeds were abundant or not (Wbp = Y or N). Habitat types are also differentiated by whether they occur near to or far from a forest edge (Edge = Y [near] or N [far]). “H.T. Code” refers to habitat type code. “Wntrr” denotes ungulate winter range, “B” denotes bison winter range, “E” denotes elk winter range, and “N” denotes areas that are not ungulate winter range. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

Table 9-1. North.

H.T. Code	Spring		Estrus		Early hyperphagia				Late hyperphagia	
	Ung = Y	Ung = N	Edge = Y	Edge = N	Wbp = Y		Wbp = N		Wbp = Y	Wbp = N
					Edge = Y	Edge = N	Edge = Y	Edge = N		
2	0.12	0.09	0.16	0.13	0.15	0.11	0.27	0.17	0.06	0.42
4	0.51	0.45	0.42	0.34	0.37	0.26	0.38	0.24	0.84	0.40
6	1.14	1.36	1.69	1.35	1.15	0.82	1.67	1.07	0.88	0.98
7	0.51	0.45	0.42	0.34	0.37	0.26	0.38	0.24	0.84	0.40
5 and 8	0.00	0.52	1.01	0.80	0.67	0.48	0.70	0.45	0.63	0.64
10100	0.12	0.09	0.31	0.25	0.15	0.11	0.06	0.04	0.13	0.21
10101	0.15	0.61	0.34	0.27	1.27	0.91	0.78	0.50	1.99	1.03
10201	0.15	0.61	0.34	0.27	1.27	0.91	0.78	0.50	1.99	1.03
10301	1.51	0.77	0.50	0.40	0.41	0.29	1.07	0.68	0.49	0.97
10401	0.12	0.05	0.09	0.07	0.36	0.26	0.54	0.34	0.31	0.47
10501	0.22	1.30	0.56	0.45	0.62	0.45	1.53	0.98	1.01	0.69
10600	1.42	2.30	1.07	0.85	1.75	1.25	3.10	1.98	1.06	0.49
10601	0.22	0.15	0.56	0.45	0.62	0.45	1.53	0.98	1.01	0.69
10701	0.27	0.23	0.63	0.50	0.68	0.49	1.20	0.76	0.86	0.87
10801	1.51	0.77	0.50	0.40	0.41	0.29	1.07	0.68	0.49	0.97

Table 9-2. East.

H.T. Code	Spring				Estrus	Early hyperphagia		Late hyperphagia			
	Ung = Y		Ung = N			Wbp = Y	Wbp = N	Wbp = Y		Wbp = N	
	Wntrr = E	Wntrr = N	Edge = Y	Edge = N				Edge = Y	Edge = N	Edge = Y	Edge = N
2	0.13	0.04	0.11	0.06	0.23	0.27	0.13	0.25	0.18	0.17	0.12
4	1.15	0.35	1.17	0.60	0.60	0.90	0.88	0.51	0.36	0.30	0.20
6	2.91	0.89	2.42	1.25	0.60	0.80	0.56	0.76	0.54	0.87	0.56
7	1.85	0.57	1.19	0.60	0.60	0.90	0.88	0.51	0.36	0.30	0.20
5 and 8	1.97	0.61	0.63	0.33	0.94	0.36	0.73	0.76	0.54	4.96	3.42
10100	1.30	0.40	1.24	0.64	0.66	0.26	0.67	0.32	0.22	0.39	0.23
10101	0.37	0.11	0.35	0.18	0.14	0.45	0.54	0.88	0.62	1.30	0.90
10201	0.16	0.05	0.65	0.34	0.23	0.55	0.49	1.38	0.98	1.26	0.95
10301	0.07	0.02	0.06	0.03	0.11	0.19	0.12	0.08	0.06	0.02	0.15
10401	0.54	0.16	0.32	0.16	0.15	0.60	0.53	1.28	0.90	1.35	0.76
10501	0.32	0.10	0.29	0.15	0.29	1.11	1.01	1.30	0.92	1.42	0.98
10600	6.15	1.89	0.67	0.34	1.67	2.61	1.79	1.11	0.79	1.73	1.19
10601	0.32	0.10	0.29	0.15	0.29	1.11	1.01	1.30	0.92	1.42	0.98
10701	1.04	0.32	0.87	0.45	0.43	0.36	0.53	0.70	0.50	0.78	0.43
10801	1.04	0.32	0.87	0.45	0.43	0.36	0.53	0.70	0.50	0.78	0.43

Table 9-3. South.

H.T.	Spring			Estrus		Early hyperphagia		Late hyperphagia		
Code	Ung = Y		Ung = N	Edge = Y	Edge = N	Wbp = Y	Wbp = N	Wbp = Y		Wbp = N
	Edge = Y	Edge = N						Edge = Y	Edge = N	
2	0.74	0.48	0.33	0.42	0.32	0.26	0.25	0.20	0.31	0.29
4	0.67	0.44	0.46	0.49	0.37	0.33	0.72	0.24	0.38	0.44
6	0.19	0.12	0.61	0.75	0.60	1.06	0.42	0.89	1.41	0.53
7	0.67	0.44	0.46	0.49	0.37	0.33	0.72	0.24	0.38	0.44
5 and 8	0.74	0.51	0.94	0.85	0.64	1.01	0.86	0.45	0.71	1.38
10100	0.74	0.49	0.33	0.42	0.32	0.26	0.25	0.20	0.31	0.29
10101	0.09	0.06	0.17	0.32	0.24	0.72	0.61	1.32	2.10	0.78
10201	0.09	0.06	0.17	0.32	0.24	0.72	0.61	1.32	2.10	0.78
10301	1.48	0.98	0.60	0.30	0.22	0.65	1.15	0.68	1.08	1.13
10401	0.37	0.25	0.12	0.35	0.27	0.38	0.35	0.44	0.71	0.48
10501	1.82	1.20	0.69	0.37	0.28	0.37	0.54	0.23	0.37	1.64
10600	0.94	0.62	0.67	0.63	0.48	0.59	0.96	0.27	0.43	0.22
10601	0.15	0.10	0.13	0.22	0.17	0.67	0.17	0.63	0.99	0.39
10701	0.86	0.57	0.45	0.70	0.53	0.68	0.95	0.48	0.77	0.68
10801	1.48	0.98	0.60	0.30	0.22	0.65	2.70	0.68	1.08	1.13

Table 9-4. West.

H.T.	Spring								Estrus		Early hyperphagia				Late hyperphagia			
Code	Ung = Y						Ung = N		Edge = Y	Edge = N	Wbp = Y		Wbp = N		Wbp = Y		Wbp = N	
	Wntrr = B		Wntrr = E		Wntrr = N		Edge = Y	Edge = N			Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N
	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N												
2	0.31	0.14	0.09	0.04	0.09	0.04	0.12	0.10	0.20	0.10	0.40	0.18	0.44	0.28	0.21	0.13	0.23	0.13
4							Missing values											
6	2.17	0.97	0.63	0.28	0.65	0.29	1.21	0.71	1.65	0.84	0.83	0.38	2.72	1.21	0.88	0.55	1.50	0.82
7							Missing values											
5 and 8	7.52	3.35	2.17	0.97	2.24	1.00	2.41	1.38	1.88	0.95	2.88	1.30	2.73	2.57	1.61	1.00	2.35	1.28
10100	0.82	0.36	0.24	0.10	0.24	0.11	0.31	0.19	0.50	0.25	0.49	0.22	0.33	0.10	0.07	0.04	0.34	0.19
10101	0.79	0.35	0.23	0.10	0.24	0.10	0.27	0.15	0.22	0.11	0.25	0.11	0.03	0.02	2.32	1.45	0.26	0.14
10201	0.79	0.35	0.23	0.10	0.24	0.10	0.27	0.15	0.22	0.11	0.25	0.11	0.03	0.02	2.32	1.45	0.26	0.14
10301	4.95	2.21	1.43	0.64	1.48	0.66	1.23	0.63	0.82	0.41	2.27	1.03	0.34	1.02	0.42	0.26	1.16	0.63
10401	0.54	0.24	0.16	0.07	0.16	0.07	0.12	0.14	0.27	0.14	0.70	0.32	3.28	0.12	0.56	0.35	0.75	0.41
10501	0.96	0.43	0.28	0.12	0.29	0.13	0.33	0.15	0.23	0.12	0.82	0.37	0.71	0.49	1.20	0.75	1.36	0.74
10600	3.94	1.76	1.14	0.51	1.18	0.52	1.50	0.90	0.88	0.44	1.09	0.49	2.21	0.61	0.40	0.25	0.34	0.19
10601	0.48	0.22	0.14	0.06	0.14	0.06	0.19	0.11	0.17	0.09	0.29	0.13	0.42	0.17	1.63	1.01	1.26	0.69
10701	1.22	0.54	0.35	0.16	0.36	0.15	0.40	0.38	1.07	0.54	0.94	0.42	1.69	0.63	1.39	0.86	1.19	0.65
10801	4.95	2.21	1.43	0.64	1.48	0.66	1.23	0.63	0.82	0.41	2.27	1.03	3.28	1.02	0.42	0.26	1.16	0.63

Appendix 10. Mean Energetic Value of a Feedsite ($avefs_{jklm}$; index)

[Years are distinguished by whether carrion was abundant or not (Ung = Y or N) and by whether whitebark pine seeds were abundant or not (Wbp = Y or N). "H.T. Code" refers to habitat type code. "Wntrr" denotes ungulate winter range, "B" denotes bison winter range, "E" denotes elk winter range, and "N" denotes areas that are not ungulate winter range. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

Table 10-1. North.

H.T. Code	Spring		Estrus	Early hyperphagia		Late hyperphagia	
	Ung = Y	Ung = N		Wbp = Y	Wbp = N	Wbp = Y	Wbp = N
2	441	101	176	223	154	120	370
4	344	48	51	91	70	60	90
6	14	116	158	249	215	503	612
7	344	48	51	91	70	60	90
5 and 8	614	1168	427	318	258	1042	1296
10100	259	101	303	223	452	102	85
10101	0	185	765	500	299	2570	1440
10201	0	185	765	500	299	2570	1440
10301	404	325	110	34	9	206	92
10401	77	185	276	99	29	1219	164
10501	713	11	258	678	635	790	788
10600	93	103	388	289	233	48	48
10601	713	11	258	678	635	790	788
10701	1322	1199	250	145	100	1397	202
10801	404	164	56	34	9	206	92

Table 10-2. East.

H.T. Code	Spring		Estrus	Early hyperphagia		Late hyperphagia	
	Ung = Y	Ung = N		Wbp = Y	Wbp = N	Wbp = Y	Wbp = N
2	313	76	176	163	159	120	370
4	189	53	51	91	70	60	86
6	4	115	158	218	215	503	609
7	29	53	51	91	70	60	86
5 and 8	773	494	429	314	258	747	913
10100	258	44	303	299	452	102	85
10101	324	5	384	331	224	862	3
10201	0	185	765	500	299	2568	1440
10301	238	408	720	85	5	926	8
10401	76	158	276	99	29	1220	164
10501	713	11	258	678	574	790	788
10600	93	103	164	289	674	48	48
10601	713	11	258	678	674	790	788
10701	404	324	110	20	9	23	93
10801	404	324	110	20	9	23	93

Table 10-3. South, without bison.

[BMUs #14, #15, and #17]

H.T. Code	Spring		Estrus	Early hyperphagia		Late hyperphagia	
	Ung = Y	Ung = N		Wbp = Y	Wbp = N	Wbp = Y	Wbp = N
2	258	34	255	290	158	121	71
4	181	138	52	9	70	59	16
6	15	110	158	98	121	515	33
7	181	138	51	9	70	59	16
5 and 8	710	1164	426	69	17	1151	699
10100	258	34	255	290	158	121	71
10101	0	185	768	484	289	2568	1410
10201	0	185	768	484	289	2568	1410
10301	404	324	110	17	2	206	13
10401	77	158	276	79	20	1220	131
10501	190	616	32	58	12	219	2
10600	92	92	164	168	138	31	23
10601	712	11	257	590	570	811	730
10701	1322	1199	248	107	62	1410	76
10801	308	324	110	17	2	206	13

Table 10-4. South, with bison.

[BMU #8]

H.T. Code	Spring		Estrus	Early hyperphagia		Late hyperphagia	
	Ung = Y	Ung = N		Wbp = Y	Wbp = N	Wbp = Y	Wbp = N
2	924	432	709	532	611	82	226
4	182	34	25	91	70	59	86
6	329	104	568	356	316	931	1036
7	182	34	25	91	70	59	86
5 and 8	303	880	665	1310	1248	458	631
10100	924	432	709	532	611	82	226
10101	0	81	771	500	299	2568	1440
10201	0	81	771	500	299	2568	1440
10301	263	185	152	34	9	206	92
10401	654	51	1261	99	28	1286	230
10501	753	663	544	1323	1303	346	206
10600	23	8	129	2200	2116	9	22
10601	0	696	18	125	119	1048	999
10701	182	34	107	186	168	1476	250
10801	263	185	152	34	9	206	92

Table 10-5. West, with bison.

[BMUs #10 and #11]

H.T. Code	Spring				Estrus	Early hyperphagia		Late hyperphagia	
	Ung = Y			Ung = N		Wbp = Y	Wbp = N	Wbp = Y	Wbp = N
	Wntrr = B	Wntrr = E	Wntrr = N						
2	726	439	439	662	1176	884	871	116	370
4					Missing values				
6	322	16	16	105	583	355	352	924	1029
7					Missing values				
5 and 8	441	819	819	898	664	1311	1248	327	603
10100	23	272	272	44	287	80	234	23	6
10101	0	0	0	82	771	500	299	2568	1440
10201	0	0	0	82	771	500	299	2568	1440
10301	263	403	403	185	120	35	9	214	92
10401	654	102	102	51	1249	99	29	1286	231
10501	753	189	189	662	544	1323	1305	346	206
10600	27	96	96	70	129	2200	2144	10	26
10601	1	713	713	706	15	125	140	1029	1025
10701	4184	1358	1358	7	1070	186	138	1468	267
10801	263	403	403	185	120	35	9	214	92

Table 10-6. West, without bison.

[BMUs #12, #13, and #18]

H.T. Code	Spring		Estrus	Early hyperphagia		Late hyperphagia	
	Ung = Y	Ung = N		Wbp = Y	Wbp = N	Wbp = Y	Wbp = N
2	439	75	176	163	216	116	370
4				Missing values			
6	16	112	173	218	215	507	612
7				Missing values			
5 and 8	819	496	426	319	258	1020	1296
10100	272	44	303	298	452	102	85
10101	0	185	765	500	299	2568	1440
10201	0	185	765	500	299	2568	1440
10301	403	210	110	35	9	214	92
10401	102	158	276	99	29	1219	164
10501	189	297	32	85	66	219	79
10600	96	82	164	289	233	31	48
10601	713	11	254	641	692	718	788
10701	1358	127	249	145	97	1388	190
10801	403	209	110	35	9	214	92

Appendix 11. Coefficients of Productivity ($coef_{jklmn}$) for the Yellowstone Grizzly Bear Cumulative Effects Model

[Years are distinguished by whether carrion was abundant or not (Ung = Y or N) and by whether whitebark pine seeds were abundant or not (Wbp = Y or N). Habitat types are also differentiated by whether they occur near or far from a forest edge (Edge = Y [near] or N [far]). “H.T. Code” refers to habitat type code. “Wntrr” denotes ungulate winter range, “E” denotes elk winter range, and “N” denotes areas that are not ungulate winter range. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

Table 11-1. North.

H.T. Code	Spring		Estrus		Early hyperphagia				Late hyperphagia	
	Ung = Y	Ung = N	Edge = Y	Edge = N	Wbp = Y		Wbp = N		Wbp = Y	Wbp = N
					Edge = Y	Edge = N	Edge = Y	Edge = N		
2	52	9	28	23	34	25	42	27	8	154
4	177	22	22	17	33	24	26	17	51	36
6	16	157	266	212	249	179	359	229	441	599
7	177	22	22	17	33	24	26	17	51	36
5 and 8	0	598	430	343	213	152	180	115	657	825
10100	178	9	94	75	34	25	26	17	14	18
10101	0	113	261	208	636	455	234	149	5112	1485
10201	0	113	261	208	636	455	234	149	5112	1485
10301	610	249	55	44	14	10	9	6	102	90
10401	9	7	26	21	36	26	15	10	374	77
10501	160	2	146	116	424	303	972	621	800	547
10600	133	237	415	331	504	361	723	462	51	24
10601	160	2	146	116	424	303	972	621	800	547
10701	358	275	157	125	99	71	119	76	1202	175
10801	610	249	55	44	14	10	9	6	102	90

Table 11-2. East.

H.T. Code	Spring				Estrus	Early hyperphagia		Late hyperphagia			
	Ung = Y		Ung = N			Wbp = Y	Wbp = N	Wbp = Y		Wbp = N	
	Wntrr = E	Wntrr = N	Edge = Y	Edge = N				Edge = Y	Edge = N	Edge = Y	Edge = N
2	41	13	8	4	40	44	20	30	22	63	45
4	217	67	63	32	29	82	61	31	22	25	17
6	10	3	280	144	94	176	119	383	271	533	339
7	53	16	63	32	29	82	61	31	22	25	17
5 and 8	1526	469	313	162	403	114	189	567	401	452	3121
10100	336	103	55	28	200	78	304	32	23	33	20
10101	120	37	2	1	55	150	120	762	539	4	3
10201	0	0	120	62	180	273	148	3542	2506	1822	1367
10301	16	5	25	13	83	16	1	74	52	0	1
10401	41	13	51	26	42	59	15	1207	1103	222	125
10501	184	36	3	2	75	753	680	1024	725	1122	774
10600	351	177	69	36	274	752	418	54	38	83	57
10601	184	36	3	2	75	753	680	1024	725	1122	774
10701	421	129	284	146	47	7	5	16	11	73	40
10801	421	129	284	146	47	7	5	16	11	73	40

Table 11-3. South, without bison.

[BMUs #14, #15, and #17]

H.T. Code	Spring			Estrus		Early hyperphagia		Late hyperphagia		
	Ung = Y		Ung = N	Edge = Y	Edge = N	Wbp = Y	Wbp = N	Wbp = Y		Wbp = N
	Edge = Y	Edge = N						Edge = Y	Edge = N	
2	192	126	11	106	80	74	40	24	38	22
4	122	80	63	25	19	3	50	14	23	6
6	3	2	67	118	90	105	51	458	726	47
7	122	80	63	25	19	3	50	14	23	6
5 and 8	550	362	1099	363	275	70	14	514	815	495
10100	192	126	11	106	80	74	40	24	38	22
10101	0	0	32	245	186	350	177	3401	5398	2964
10201	0	0	32	245	186	350	177	3401	5398	2964
10301	601	395	196	32	25	11	3	140	222	14
10401	29	19	19	97	73	30	7	543	861	93
10501	346	228	418	12	9	22	6	51	81	1
10600	87	57	62	103	78	99	133	8	13	10
10601	106	70	1	57	43	395	94	508	806	726
10701	1143	752	537	175	133	72	59	683	1082	58
10801	601	395	196	32	25	11	3	140	222	14

Table 11-4. South, with bison.

[BMU #8]

H.T. Code	Spring			Estrus		Early hyperphagia		Late hyperphagia		
	Ung = Y		Ung = N	Edge = Y	Edge = N	Wbp = Y	Wbp = N	Wbp = Y		Wbp = N
	Edge = Y	Edge = N						Edge = Y	Edge = N	
2	687	452	145	294	223	136	156	16	25	65
4	123	81	16	12	9	30	50	14	23	38
6	61	41	64	426	323	378	133	828	1314	553
7	123	81	16	12	9	30	50	14	23	38
5 and 8	235	154	831	565	429	1321	1073	205	324	874
10100	687	452	145	294	223	136	156	16	25	65
10101	0	0	14	247	187	362	183	3401	5398	1123
10201	0	0	14	247	187	362	183	3401	5398	1123
10301	391	228	112	45	34	22	10	140	222	104
10401	245	162	6	441	335	37	10	572	908	110
10501	1370	902	458	199	151	491	700	80	127	338
10600	22	14	6	81	62	1305	2038	3	4	5
10601	0	0	88	4	3	84	20	656	1041	388
10701	157	103	15	752	570	126	159	714	1133	170
10801	391	228	112	45	34	22	10	140	222	104

Table 11-5. West, with bison.

[BMUs #10 and #11]

H.T. Code	Spring								Estrus		Early hyperphagia				Late hyperphagia			
	Ung = Y						Ung = N				Wbp = Y		Wbp = N		Wbp = Y		Wbp = N	
	Wntrr = B		Wntrr = E		Wntrr = N													
	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N
2	222	99	39	17	40	18	80	63	236	120	357	162	383	247	24	15	87	47
4	Missing values																	
6	698	311	10	5	10	5	126	74	962	488	296	134	958	427	817	509	1544	841
7	Missing values																	
5 and 8	3316	1478	1779	793	1837	819	2164	1241	1248	634	3773	1705	3408	3212	525	327	1415	770
10100	19	8	64	29	66	30	14	8	144	73	39	18	78	24	2	1	2	1
10101	0	0	0	0	0	0	22	13	166	85	125	57	10	5	5966	3714	380	207
10201	0	0	0	0	0	0	22	13	166	85	125	57	10	5	5966	3714	380	207
10301	1302	580	576	257	595	265	227	117	98	50	80	36	29	9	90	56	107	58
10401	353	157	16	7	16	7	6	7	339	172	69	31	10	3	724	451	174	95
10501	726	324	53	23	54	24	217	100	125	64	1087	492	932	642	416	259	280	152
10600	107	48	110	49	113	51	106	63	114	58	2395	1083	4743	1312	4	2	0	0
10601	0	0	99	44	103	46	132	76	3	1	37	17	58	24	1677	1044	1296	705
10701	224	100	477	212	492	205	3	3	1145	581	175	79	234	87	2038	1269	317	172
10801	1302	580	576	257	595	265	227	117	98	50	80	36	29	9	90	56	107	58

Table 11-6. West, without bison.

[BMUs #12, #13, and #18]

H.T.	Spring				Estrus		Early hyperphagia				Late hyperphagia			
Code	Ung = Y		Ung = N		Edge = Y	Edge = N	Wbp = Y		Wbp = N		Wbp = Y		Wbp = N	
	Edge = Y	Edge = N	Edge = Y	Edge = N			Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N
2	40	18	9	7	35	18	66	30	95	61	24	15	87	47
4								Missing values						
6	10	5	135	79	285	145	182	82	584	260	449	279	919	500
7								Missing values						
5 and 8	1837	819	1195	686	801	407	919	415	704	663	1639	1021	3044	1657
10100	66	30	14	8	152	77	145	66	151	47	7	4	29	16
10101	0	0	50	29	165	84	125	57	10	5	5966	3714	380	207
10201	0	0	50	29	165	84	125	57	10	5	5966	3714	380	207
10301	595	265	50	132	89	45	80	36	29	9	90	56	107	58
10401	16	7	19	22	75	38	69	31	10	3	687	428	124	68
10501	54	24	19	45	7	4	70	31	48	33	263	164	108	58
10600	113	51	97	74	144	73	314	142	515	142	13	8	0	0
10601	103	46	123	1	44	23	189	85	289	119	1171	729	996	542
10701	492	205	2	49	266	135	137	62	165	61	1928	1200	225	123
10801	595	265	50	132	89	45	80	36	29	9	90	56	107	58

Appendix 12. Coefficients of Productivity ($coef_{jklmn}$) for the Yellowstone Grizzly Bear Cumulative Effects Model, Averaged Over Year Types Within Seasons

[“H.T. Code” refers to habitat type code. “Wntrr” denotes ungulate winter range, “B” denotes bison winter range, “E” denotes elk winter range, and “N” denotes areas that are not ungulate winter range. Values are missing in the table if corresponding habitat types were not present in a region or were so sparse as to be consolidated with another type]

Table 12-1. North.

H.T. Code	Spring	Estrus		Early hyperphagia		Late hyperphagia
		Edge = Y	Edge = N	Edge = Y	Edge = N	
2	31	28	23	38	26	81
4	99	22	17	30	20	43
6	87	266	212	304	204	520
7	99	22	17	30	20	43
5 and 8	299	430	343	197	134	741
10100	93	94	75	30	21	16
10101	56	261	208	435	302	3298
10201	56	261	208	435	302	3298
10301	429	55	44	12	8	96
10401	8	26	21	25	18	225
10501	81	146	116	698	462	674
10600	185	415	331	614	412	37
10601	81	146	116	698	462	674
10701	316	157	125	109	74	688
10801	429	55	44	12	8	96

Table 12-2. East.

H.T. Code	Spring				Estrus	Early hyperphagia	Late hyperphagia	
	Wntrr = E		Wntrr = N				Edge = Y	Edge = N
	Edge = Y	Edge = N	Edge = Y	Edge = N				
2	25	23	11	8	40	32	47	33
4	140	125	65	50	29	72	28	20
6	145	77	141	74	94	147	458	305
7	58	43	40	24	29	72	28	20
5 and 8	920	844	391	315	403	151	2547	1761
10100	196	182	79	66	200	191	33	21
10101	61	60	19	19	55	135	383	271
10201	60	31	60	31	180	211	2682	1936
10301	20	14	15	9	83	8	37	27
10401	46	34	32	19	42	37	714	614
10501	94	93	20	19	75	717	1073	749
10600	210	193	123	106	274	585	68	48
10601	94	93	20	19	75	717	1073	749
10701	352	284	207	138	47	6	44	26
10801	352	284	207	138	47	6	44	26

Table 12-3. South, without bison.

[BMUs #14, #15, and #17]

H.T. Code	Spring		Estrus		Early hyperphagia	Late hyperphagia	
	Edge = Y	Edge = N	Edge = Y	Edge = N		Edge = Y	Edge = N
2	101	69	106	80	57	23	30
4	93	72	25	19	27	10	14
6	35	34	118	90	78	252	387
7	93	72	25	19	27	10	14
5 and 8	824	730	363	275	42	505	655
10100	101	69	106	80	57	23	30
10101	16	16	245	186	264	3183	4181
10201	16	16	245	186	264	3183	4181
10301	399	296	32	25	7	77	118
10401	24	19	97	73	18	318	477
10501	382	323	12	9	14	26	41
10600	74	59	103	78	116	9	12
10601	54	35	57	43	244	617	766
10701	840	644	175	133	66	370	570
10801	399	296	32	25	7	77	118

Table 12-4. South, with bison.

[BMU #8]

H.T. Code	Spring		Estrus		Early hyperphagia	Late hyperphagia	
	Edge = Y	Edge = N	Edge = Y	Edge = N		Edge = Y	Edge = N
2	416	298	294	223	146	41	45
4	69	48	12	9	40	26	30
6	63	52	426	323	255	690	934
7	69	48	12	9	40	26	30
5 and 8	533	493	565	429	1197	539	599
10100	416	298	294	223	146	41	45
10101	7	7	247	187	273	2262	3261
10201	7	7	247	187	273	2262	3261
10301	251	170	45	34	16	122	163
10401	126	84	441	335	24	341	509
10501	914	680	199	151	595	209	233
10600	14	10	81	62	1672	4	4
10601	44	44	4	3	52	522	715
10701	86	59	752	570	143	442	651
10801	251	170	45	34	16	122	163

Table 12-5. West, with bison.

[BMUs #10 and #11]

H.T.	Spring						Estrus		Early hyperphagia		Late hyperphagia	
Code	Wntrr = B		Wntrr = E		Wntrr = N		Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N
	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N						
2	151	81	60	40	60	40	236	120	370	204	55	31
4	Missing values											
6	412	193	68	39	68	39	962	488	627	280	1180	675
7	Missing values											
5 and 8	2740	1360	1971	1017	2000	1030	1248	634	3590	2458	970	549
10100	16	8	39	18	40	19	144	73	59	21	2	1
10101	11	6	11	6	11	6	166	85	68	31	3173	1960
10201	11	6	11	6	11	6	166	85	68	31	3173	1960
10301	764	349	402	187	411	191	98	50	54	23	98	57
10401	180	82	11	7	11	7	339	172	39	17	449	273
10501	471	212	135	62	136	62	125	64	1010	567	348	206
10600	107	56	108	56	110	57	114	58	3569	1197	2	1
10601	66	38	116	60	117	61	3	1	48	20	1487	875
10701	113	51	240	108	248	104	1145	581	204	83	1178	721
10801	764	349	402	187	411	191	98	50	54	23	98	57

Table 12-6. West, without bison.

[BMUs #12, #13, and #18]

H.T. Code	Spring		Estrus		Early hyperphagia		Late hyperphagia	
	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N	Edge = Y	Edge = N
2	25	13	35	18	80	46	55	31
4				Missing values				
6	73	42	285	145	383	171	684	390
7				Missing values				
5 and 8	1516	752	801	407	811	539	2341	1339
10100	40	19	152	77	148	56	18	10
10101	25	14	165	84	68	31	3173	1960
10201	25	14	165	84	68	31	3173	1960
10301	323	199	89	45	54	23	98	57
10401	18	14	75	38	39	17	405	248
10501	37	34	7	4	59	32	185	111
10600	105	62	144	73	414	142	6	4
10601	113	23	44	23	239	102	1083	635
10701	247	127	266	135	151	61	1077	661
10801	323	199	89	45	54	23	98	57

Published in the Central Region, Lafayette, Louisiana.

USGS Publishing Staff: Charron, T., Davis, R., Farris, G., Lauritzen, S., Vairin, B.

Johnson Controls, Inc. Staff: Trahan, N., Wiggins, L.