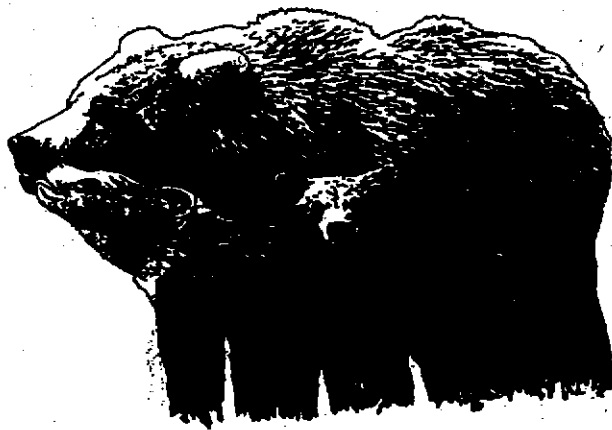

Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*)

Dissertation

by David J. Mattson



April 2000

CAUSES AND CONSEQUENCES OF DIETARY DIFFERENCES AMONG
YELLOWSTONE GRIZZLY BEARS (*URSUS ARCTOS*)

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

with a

Major in Forestry, Wildlife, and Range Sciences

in the

College of Graduate Studies

University of Idaho

by

David J. Mattson

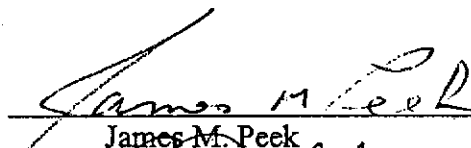
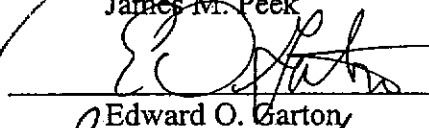
April 2000

Major Professor: James M. Peek, Ph.D.

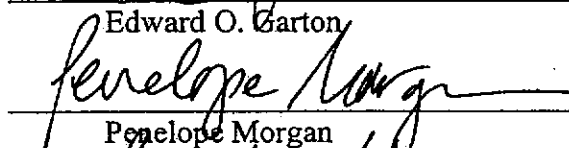
AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of David J. Mattson, submitted for the degree of Doctor of Philosophy with a major in Fish and Wildlife Resources and titled "Causes and Consequences of Dietary Differences Among Yellowstone Grizzly Bears (*Ursus arctos*)," has been reviewed in final form, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

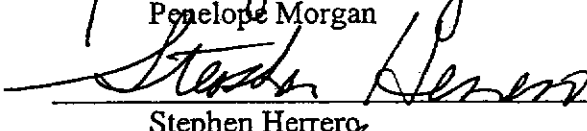
Major Professor


Date 28 Mar 00Committee
Members

Date 3/28/00

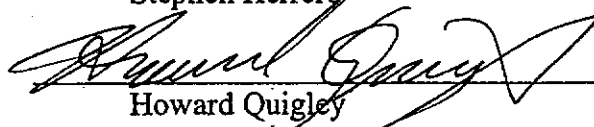
Edward O. Garton


Date 3/28/00

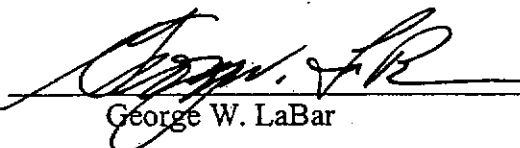
Penelope Morgan


Date ✓

Stephen Herrero


Date 3/28/00

Howard Quigley

Department
Administrator

Date 3/28/00

George W. LaBar

Discipline's
College Dean

Date 3/28/00

Charles R. Hatch

Final Approval and Acceptance by the College of Graduate Studies

Date _____

Charles R. Hatch

ABSTRACT

Little is known about how the diets and behaviors of grizzly bears (*Ursus arctos horribilis*) reflect habitat conditions and how, in turn, diet and behavior affect the movement, size, condition, and reproduction of individual animals. No study has collected detailed information on all of these facets of grizzly bear ecology over a span of time and space sufficient to represent conditions affecting a population of bears. Detailed information on how and why habitat affects the movements and reproduction of bears is important to reliably anticipating the effects of management and environmental change.

I participated in a study of grizzly bears in the 23,000-km² Yellowstone ecosystem from 1979 to 1992. During this study, field crews visited over 1800 telemetry locations of radiomarked animals and collected information on site features and activity of the marked bear. I used this information, along with information on general habitat conditions and movements, gross morphology, and reproduction of individual bears, to test research hypotheses derived from conceptual models. I hypothesized that female bears who ate more whitebark pine (*Pinus albicaulis*) seeds and fewer roots would be more fecund than females who did not. I also hypothesized that, compared to males, females would eat greater amounts of fatty foods and, compared to females, males would eat greater amounts of proteinaceous foods. Whitebark pine seeds are the most abundant fatty food and ungulates the most abundant proteinaceous food of grizzly bears in the Yellowstone ecosystem.

This study's results were broadly consistent with both hypotheses. After mid-July, male grizzly bears more often exploited ungulate carcasses compared to females. Bears consumed maximum amounts from each carcass during this late-season period, at a time when ungulates had accumulated maximum adipose reserves and bears obtained most ungulate tissue by predation. Females ate pine seeds about twice as often as did males. Compared to females who ate more roots, females who ate more pine seeds were more likely to have 3-cub litters and reproduce first at an earlier age. Females who more often ate concentrated proteinaceous or fatty foods more often lost cubs compared to females who did not, probably due to infanticide by other adult bears. By contrast, females who frequently ate dispersed low-quality foods, such as ants, lost few cubs. Segregation of the sexes observed during this study was probably due to different dietary preferences as well as the threat of infanticide posed by adult male bears.

ACKNOWLEDGEMENTS

First and foremost I thank my wife, Susan Bischoff, for her steadfast love, support, and patience over my many days and months of absences following bear sign and writing this dissertation. My sons, Zachary and Sky, kept my life in balance. My parents, Donald and Maxine Mattson, gave me complete acceptance and the confidence to follow my passions. My major professor, James Peek, offered me a masterful mix of wisdom, support, patience, and prodding. Gerry Wright, Oz Garton, and Kirk Steinhorst enriched my tenure at the University of Idaho. Steve Herrero and Steve Stringham enriched and broadened my thinking about bears, their evolution, and the places they live. Dave Burrup, Linda Cayot, Dave Delsordo, Doug Dunbar, Gerry Green, Mark Haroldson, Jeff Henry, Bill Hoskins, Carrie Hunt, Jamie Jonkel, Kate Kendall, Mike Knapp, Jim Orpet, Dan Reinhart, Bart Schleyer, Erin Shannahan, Roger Swalley, and others trapped bears, visited radiotelemetry locations, and otherwise collected data used in this dissertation. More important, they were companions and friends. Funding for this research was provided by the U.S. National Park Service, Wyoming Department of Game & Fish, U.S. Fish & Wildlife Service, U.S. National Biological Service, and U.S.G.S. Biological Resources Division. Gerry Wright and Mike Collopy generously supported the completion of this work. Richard Knight supervised the Interagency Grizzly Bear Study Team during this study.

TABLE OF CONTENTS

	Page
AUTHORIZATION TO SUBMIT DISSERTATION	ii
ABSTRACT	iii
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	xii
INTRODUCTION	1
Theoretical models of grizzly bear fecundity and feeding	2
Fecundity of male grizzly bears	6
Fecundity of female grizzly bears	8
Other theoretical considerations	11
Diet composition in Yellowstone	12
STUDY AREA	15
METHODS	16
Field methods	16
Trapping, measurement, and relocation	16
Site features and activities of grizzly bears at telemetry relocations	16
Nutrient content of bear foods	17
Analysis methods and considerations	18
Sampling units and independence	18
Model selection	19
Derived response variables	20
Home range size and movements	21
Corpulence	22
Lean body volume	24
Reproduction	24
Derived or distal independent variables	25
Class variables	25
Continuous variables	33
Statistical models	36
Home range size and movements	36
Corpulence and body size	36
Reproduction	37
Likelihood and levels of different activities	38

TABLE OF CONTENTS (continued)

RESULTS	41
Activities	41
Use of whitebark pine seeds	41
Use of ungulates	46
Use of roots	51
Use of high-quality grazed foods	60
Use of fibrous vegetal foods	67
Use of ants	72
Use of rodents and rodent food caches	79
Use of mushrooms	86
Use of berries	86
Bedding	86
No sign of feeding or bedding	92
Differences among bear classes in use of habitats	92
Females with COY compared to other classes	92
Adult males compared to other classes	97
Activities of individual males and females	101
Range sizes and movements	101
Corpulence and relative lean body volume	105
Female reproduction	110
Correlations among activities	115
DISCUSSION	116
Biases and bias control	116
Non-dietary effects on movements, morphology, and female reproduction	119
Causes and consequences of dietary differences	120
Use of whitebark pine seeds	120
Use of ungulates and other proteinaceous foods	125
Use of roots	131
Use of rodents and rodent food caches	133
Use of ants and other Hymenoptera	135
Use of grazed foods	136
Effects of avoidance, competition, and population density	138
Habitat segregation	138
Density dependence, competition, and density independence	140
Projected effects of environmental change	144
Effects of wolves	144
Effects of climate change and fire	146
REFERENCES	151

LIST OF TABLES

Table		Page
1	Description of activity types used in the analysis of relations between activities of individual bears and their movements, morphological characteristics, and reproduction	28
2	Description of habitat and winter range types used to map grizzly bear habitat in the Yellowstone area and used to analyze patterns of activities by Yellowstone's grizzly bears	29
3	Percent occurrence of different activities by habitat types, for radio-marked Yellowstone grizzly bears, 1977-92	30
4	Percent cover of habitat and winter range types in Bear Management Units (BMUs) of the Yellowstone area	31
5	Annual values of distal independent variables used in the analysis of grizzly bear activities and female grizzly bear reproduction in the Yellowstone area, 1977-92	34
6	Estimated percent frequency of feeding activities by female grizzly bears, 1977-92, in different regions of the Yellowstone area defined on the basis of Bear Management Units (BMUs)	39
7	Logistic regression models for the logit-transformed probability that a bear had been feeding on whitebark pine seeds, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, vegetation features, type of bear, and time	42
8	Multiple regression models of the relations of extent of excavations or number of cones per dm ³ of excavation for whitebark pine cones at a site where feeding of this type occurred, to food abundance, temperatures, and time	43
9	Logistic regression models for the logit-transformed probability that a bear had been feeding on an ungulate carcass, related to variables pertaining to distal effects including carcass numbers, extent of habitat types, weather, and type of bear	47
10	Logistic regression models for the logit-transformed probability that a bear had been feeding on an ungulate carcass, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, vegetation and site features, and weather	49

LIST OF TABLES (continued)

Table		Page
11	Multiple regression models of the relations of amount of ungulate tissue consumed at a site where feeding of this type occurred, to carcass type, vegetation features age class of bear, and time	52
12	Logistic regression models for the logit-transformed probability that a bear had been feeding on roots of yampa, biscuitroot, or osmorhiza, related to variables pertaining to distal effects including food availability, extent of habitat types, weather, type of bear, and date	53
13	Logistic regression models for the logit-transformed probability that a bear had been feeding on roots of yampa, biscuitroot, or osmorhiza, related to variables pertaining to distal and proximal effects including extent of habitat types, food abundance, vegetation features, elevation, weather, gender, and time	58
14	Multiple regression models of the relations of number of excavations or number of plants per excavation for yampa, biscuitroot, or osmorhiza roots at a site where feeding on this food occurred, to food abundance, vegetation features, elevation, weather, age class of bear, and date	59
15	Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (spring or estrus), clover, or dandelions, related to variables pertaining to distal effects including food availability, extent of habitat types, weather, type of bear, and time	63
16	Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (spring or estrus), clover, or dandelions, related to variables pertaining to distal and proximal effects, including food availability, extent of habitat types, food abundance, vegetation features, and time	64
17	Logistic or multiple regression models of the relations of number of feces observed at a site where feeding on clover or dandelion occurred or of the probability that a feces had been present at a site where grazing on early season graminoids had occurred, to number of ungulate carcasses, extent of bison winter range, food abundance and phenology, vegetation features, weather, type of bear, and time	65
18	Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (Hyperphagia) or thistles related to variables pertaining to distal effects including food availability, the extent of habitat types, weather, age class of bear, and time period	68

LIST OF TABLES (continued)

Table	Page
19	Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (hyperphagia) or thistles, related to variables pertaining to distal and proximal effects including food availability, the extent of habitat types, food abundance at the site, vegetation and site features, and weather 70
20	Multiple regression models of the relations of number of feces observed or stems consumed at a site where feeding on either graminoids (Hyperphagia) or thistle occurred, to food abundance, vegetation and site features, and weather 73
21	Logistic regression models for the logit-transformed probability that a bear had been feeding on ants in dirt/debris hills, related to variables pertaining to distal and proximal effects including extent of habitat types, vegetation and site features, weather, and time 75
22	Logistic regression models for the logit-transformed probability that a bear had been feeding on ants in logs, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, vegetation and site features, weather, and time 76
23	Multiple regression models of the relations of number of excavations or mean size of excavation for ants in logs or hills at a site where feeding of this type occurred, to vegetation and site features 77
24	Logistic regression models for the logit-transformed probability that a bear had been feeding on rodents or rodent food caches during Spring and Estrus, related to variables pertaining to distal and proximal effects including number of bison, extent of habitat types, location within a habitat type, vegetation features, winter ppt, and time 80
25	Multiple regression models of the relations of volume of excavations for rodents or number of nests or root caches per unit volume of excavation at a site where feeding on rodents occurred during Spring or Estrus, to species abundance, vegetation and site features, and age-class of bear 82
26	Logistic regression models for the logit-transformed probability that a bear had been feeding on rodents or rodent food caches during Hyperphagia, related to variables pertaining to distal and proximal effects including location within a habitat type, vegetation features, weather, and time period 83
27	Multiple regression models of the relations of volume of excavations for rodents or number of nests or root caches per unit volume of excavation at a site where feeding on rodents occurred during Hyperphagia, to species abundance and slope . 85

LIST OF TABLES (continued)

Table	Page
28 Multiple regression models of relations of the logit-transformed probability that a bear had been feeding on mushrooms or of number of excavations for mushrooms at a site where this feeding occurred, to food abundance, extent of habitat types, vegetation and site features, weather, type of bear, and time	88
29 Logistic regression models for the logit-transformed probability that a bear had been feeding on berries, related to variables pertaining to distal and proximal effects including food abundance, extent of habitat type, vegetation features, weather, type of bear, and time	89
30 Logistic regression models for the logit-transformed probability that sign of bedding was found at a telemetry location, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, site and vegetation features, weather, and type of bear	90
31 Logistic regression models for the logit-transformed probability that no sign of feeding or bedding was found at a telemetry location, related to variables pertaining to distal and proximal effects including food availability, site and vegetation features, weather, type of bear, and time	93
32 Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult female with cubs-of-the-year versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Spring and Estrus	94
33 Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult female with cubs-of-the-year versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Hyperphagia	95
34 Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult male versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Spring & Estrus	98
35 Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult male versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Hyperphagia	99
36 The proportion of activities at radiotelemetry locations and variation in those proportions among individuals, by gender, for individual Yellowstone grizzly bears	103

LIST OF TABLES (continued)

Table		Page
37	Regression models for the relations of movements and multi-annual range sizes (50% and 95%) to effect of management translocation, number of telemetry locations, body size, % of locations by reproductive status, % of locations by season, and activity	104
38	Regression models for relations of body morphology to movements, date, % of relocations by reproductive status, and activity of female grizzly bears	107
39	Regression models for relations of body morphology to date, % of relocations obtained as a subadult, and activity of male grizzly bears	108
40	Regression models for the relations of number of cubs observed and number of cubs subsequently lost, by individual bear, to duration of observations per bear, median maternal age, and maternal activity, for female grizzly bears	111
41	Logistic regression models of the annual probability of producing a litter, and given a litter, the probability that the litter consisted of 1 or 3 cubs and that at least one cub was lost to natural causes, related to maternal age, food availability, and maternal activity, for female grizzly bears	112

LIST OF FIGURES

Figure		Page
1	A theoretical model of factors and relations affecting the fecundities of male and female grizzly bears, with an emphasis on the roles of lean body mass and adipose reserves	3
2	A theoretical model of factors and relations affecting the fecundity of female grizzly bears, with an emphasis on the role of adipose reserves and dietary fat	4
3	A theoretical model of factors and relations influencing the use of foods by Yellowstone grizzly bears, 1977-92	5
4	Measurements used to calculate morphometric indices for Yellowstone's grizzly bears	23
5	Results of clustering Yellowstone grizzly bear foods based on energetic and nutritional characteristics of the foods	27
6	Map of the Yellowstone study area showing the outer boundary of the Recovery Area, boundaries of individual Bear Management Units within, and the boundary of Yellowstone National Park	32
7	Relations between grizzly bear use of whitebark pine seeds and variables denoting vegetation structure or abundance of seeds	44
8	Relations between grizzly bear use of whitebark pine seeds and variables denoting distal effects of landscape features, food abundance, date, gender, and the fires of 1988	45
9	Relations between grizzly bear use of ungulates and variables denoting effects of season, gender, ungulate carcass availability, weather, and extent of whortleberry-type forests	48
10	Relations between grizzly bear use of ungulates and variables denoting effects of forb or graminoid cover and date	50
11	Relations between grizzly bear use of yampa and biscuitroot roots and variables denoting effects of season and class-of-bear	54
12	Relations between grizzly bear use of various roots and variables denoting effects of weather	55
13	Relations between grizzly bear use of various roots and variables denoting effects of species abundance and elevation at a feeding site as well as extent of mesic non-forest sites in the surrounding BMU	56

LIST OF FIGURES (continued)

Figure	Page
14	Relations between grizzly bear use of various roots and variables denoting effects of vegetation structure and cover at a feeding site 57
15	Relations between grizzly bear use of osmorhiza roots and variables denoting effects of the size of the whitebark pine cone crop, date, and extent of mesic subalpine fir forests in the surrounding BMU 61
16	Relations between grizzly bear grazing of clover, dandelions, and early-season graminoids and variables denoting effects of the extent of ungulate winter range in the surrounding BMU, elk numbers, and weather 62
17	Relations between grizzly bear grazing of clover, dandelion and early-season graminoids and variables denoting effects species abundance and phenology 66
18	Relations between grizzly bear grazing of fibrous foods and variables denoting effects of number of elk in the ecosystem, temperature, and elevation 69
19	Relations between grizzly bear grazing of fibrous foods and variables denoting effects of species abundance, vegetation cover, and distance to forest 71
20	Relations between grizzly bear use of ants from logs and hills and variables denoting effects of extent of mesic non-forest in the surrounding BMU, number of bison in ecosystem, temperature, and date 74
21	Relations between grizzly bear use of ants in logs and hills and variables denoting effects of forest structure 78
22	Relations between grizzly bear use of rodents or rodent food caches during Spring and Estrus and variables denoting effects of vegetation features, slope, winter ppt, and date 81
23	Relations between grizzly bear use of rodents or rodent food caches during Hyperphagia and variables denoting effects of graminoid cover and species abundance 84
24	Relations between grizzly bear use of mushrooms and variables denoting effects of the extent of habitat types in the surrounding BMU, date, lodgepole pine basal area, and total vegetation ground cover 87
25	Relations between bedding or the absence of feeding sign at a bear location and variables denoting number of elk in ecosystem, date, reproductive status or co-occurrence of feeding on ungulates, and forest basal area 91

LIST OF FIGURES (continued)

Figure		Page
26	Relations between the likelihood that a female with cubs-of-the-year had been located versus other classes of bears during Spring and Estrus and during Hyperphagia relative to the extent of whitebark pine forests in the surrounding BMU	96
27	Relations between the likelihood that an adult male had been located versus other classes of bears during Spring and Estrus relative to the extent of habitat types in the surrounding BMU, elevation, and forest basal area	100
28	Relations between the likelihood that an adult male had been located versus other classes of bears during Hyperphagia relative to the extent of habitat types in the surrounding BMU, slope, yampa abundance, and the extent of shrub cover	102
29	Relations between 95% home range size and proportion of locations obtained from females during Estrus and 50% home range size and relative lean body mass of males	106
30	Relations between Julian date and corpulence of females, and between the consumption of roots and corpulence of males and relative lean body mass of females	109
31	Relation between the proportion of years that a female was observed with cubs and her age	113
32	Relations between proportions of litters with 1 or 3 cubs observed with female grizzly bears and age of the dam, extent of whitebark pine forests in the surrounding BMU, or size of the whitebark pine cone crop the previous year	114
33	A theoretical model showing density- and food-related factors and relations affecting reproduction and survival of Yellowstone grizzly bears	141

Introduction

The grizzly bear (*Ursus arctos horribilis*) population occupying the Yellowstone ecosystem of the western United States of America (U.S.) is small and isolated. The population likely numbers 300–400 individuals (Eberhardt & Knight, 1996) and is about 250 km from the nearest population of conspecifics (Mattson *et al.*, 1995). In 1975, these conditions combined with habitat degradation and high levels of mortality led to designation of the Yellowstone population as ‘threatened’ under the U.S. Endangered Species Act. Drs. John and Frank Craighead pioneered research on this population from 1959 to 1970. The ‘threatened’ designation together with controversies accompanying termination of the Craigheads’ research program (Craighead, Sumner & Mitchell, 1995) provided impetus for research conducted by the Interagency Grizzly Bear Study Team that has lasted from 1974 to the present.

Despite the extent of research during this 36 years on diet, habitat use, and demography, scientists have not directly addressed some potentially critical issues for management and survival of the Yellowstone grizzly bear population. With the exception of the analysis by Craighead *et al.* (1995), much of what has been reported to date on the causes and consequences of dietary differences among bears has been descriptive and, thus, constitutes an uncertain basis for anticipating the consequences of natural or human-induced perturbations. Even where the emphasis has been on explanation, habitat-related work has focused on use of specific foods or habitat complexes by bears and has not often linked diet and habitat use to movements or reproductive success (Blanchard & Knight, 1991; Mattson, Blanchard & Knight, 1992a; Mattson & Reinhart, 1995). Research from Yellowstone (Mattson *et al.*, 1987, 1992a) also has suggested that different classes of bears (by sex, age, and parturient status) are distributed differently relative to human facilities. However, a comprehensive investigation of these distributions has not been undertaken.

This dissertation focuses on the following questions: (1) How are movement, size, and reproduction of bears related to their diets?, (2) How are diet and habitat use related to food availability and sex, age, and parturient status of the bear?, and (3) Why do these relations exist? I used data collected 1977–92 from radiomarked grizzly bears in the Yellowstone ecosystem to address these questions by empirically testing theoretical models

derived from prior research. I also used these data to explore relations that were unknown or otherwise more uncertain.

Theoretical models of grizzly bear fecundity and feeding

I used data that were collected as part of an observational study (*sensu* Eberhardt & Thomas, 1991). Strictly speaking, there were no controls or manipulations. Under such conditions the validity of any causal inference, at best conjectural, relies upon a dialectic of theoretical models and empirical tests — introducing ‘controls’ and deriving conditional independence of observations via biologically plausible statistical models (Wold, 1956; Dawid, 1979; Rosenbaum, 1984; Hilborn & Mangel, 1997; Burnham & Anderson, 1998). Without systematized expectations derived from previous scientific work (i.e., a theoretical model), hypotheses are more often unenlightening, statistical models more often suffer from specification error, analysis more often yields spurious results, and misinterpretation of associations is more likely to damage managed resources and impede scientific progress (Hilborn & Mangel, 1997; Burnham & Anderson, 1998).

For these reasons, I structured the analysis presented in this dissertation according to theoretical models (Figs. 1–3). These models are as replete as possible — to aid design and interpretation of the analysis — but do not include factors and relations that were implausible or that had been shown to be trivial by previous research. Because little is known about some aspects of bear physiology and behavior, I used other medium-sized to large omnivores (e.g., swine [*Sus scrofa*] and primates) as models for some theorized relations regarding growth and metabolism.

The first two theoretical models (Figs. 1 & 2) focus on reproductive success of male and female grizzly bears. These models are conjectures regarding the causes and consequences of dietary differences between the sexes. I assume that gender-specific differences in nutritional needs (fitness consequences) selected for sex-linked differences in dietary preferences (causes). Such evolutionary processes transcend the scale at which cause-and-effect were investigated in this analysis. The models of reproductive success constitute a basis for expecting sex-linked differences in dietary preference and habitat use. I incorporated these expectations into a third model (Fig. 3) focusing on grizzly bear diets in Yellowstone. This third model provides a framework for statistical analysis and is the focus

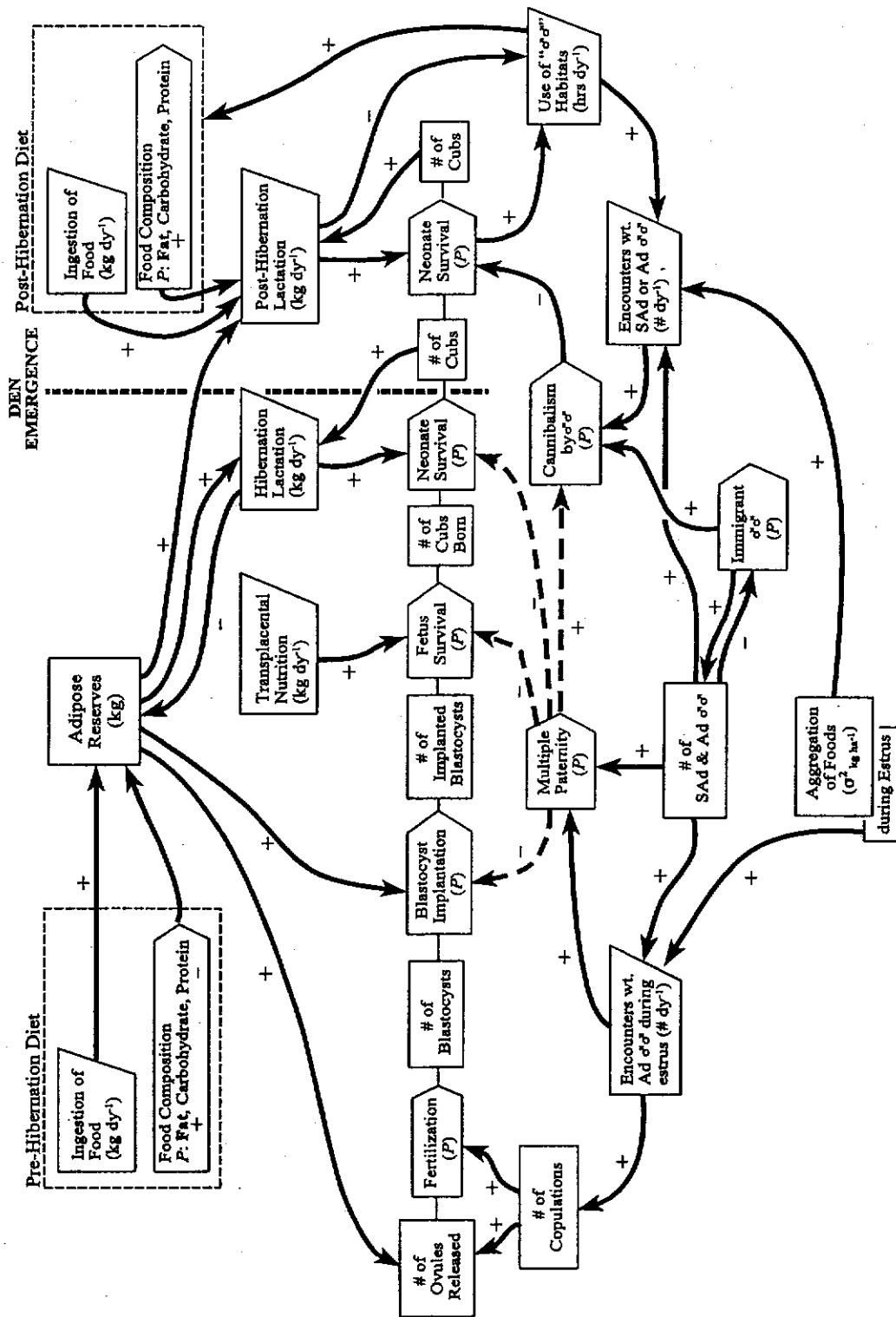


FIG. 2. A theoretical model of factors and relations affecting the reproductive success of female grizzly bears, with an emphasis on the role of adipose reserves and dietary fat. Reproductive success is construed as survival of offspring to independence. Dashed arrows indicate relations that are likely to be weak or that have an uncertain basis in previous research. 'SAd' denotes subadult and 'Ad' denotes adult. The '+' and '-' denote the nature of response with an increase in the influencing factor. Rectangles represent states, arrowed boxes represent transitions (probabilities), and boxes with a skewed right margin represent rates.

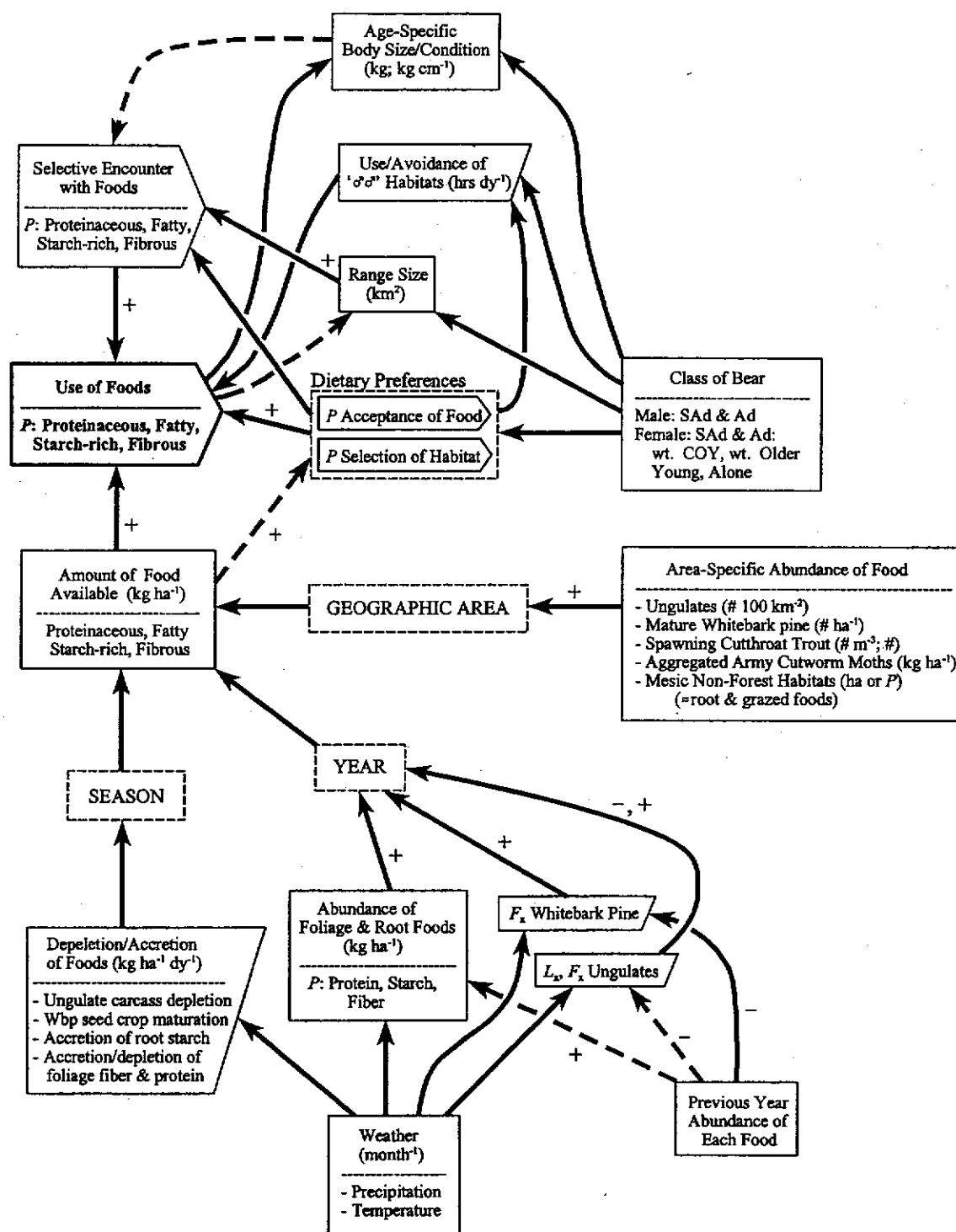


FIG 3. A theoretical model of factors and relations influencing the use of foods by Yellowstone grizzly bears, 1977–92. Dashed boxes indicate factors that are used as surrogates for other variables that more directly determine the amount of food available. Dashed arrows indicate relations that are likely to be weak or that have an uncertain basis in previous research. 'SAd' denotes subadult and 'Ad' denotes adult. The '+'s and '-'s denote the nature of response with an increase in the influencing factor. Rectangles represent states, arrowed boxes represent transitions (probabilities), and boxes with a right skewed margin represent rates.

of this dissertation. I used the first two models principally as conceptual foundations and aids in interpretation.

Reproductive success of male grizzly bears

Little is currently known about the reproductive success of male bears (construed here as number of fertilized ova) and the factors associated with this success. However, there are several reasons to theorize that lean body mass and dietary protein have critical influences (Fig. 1). For one, the mass of bear testes is positively correlated with age and total body mass (Erickson *et al.*, 1968; Tsubota & Kanagawa, 1989; White, Berardinelli & Aune, 1998).

Furthermore, sperm production in mammals is positively correlated with mass of the testes (Harvey & Harcourt, 1984; Tsubota & Kanagawa, 1989). Probability of fertilization also increases with ejaculate volume (Harvey & Harcourt, 1984; Parker, 1984). Consequently, larger male body size likely increases reproductive success by enhancing sperm competitiveness in the promiscuous breeding system typical of bears (Craighead *et al.*, 1995; L. Craighead *et al.*, 1995; Schenk & Kovacs, 1995).

Large lean body mass also may increase frequency of encounters and copulations by males with estrus females. For bears and other large mammals, frequency of access to reproductive females by males is often a function of social dominance, in turn positively related to body size (Manning, 1985; for grizzly bears, Craighead *et al.*, 1995; for elephant seals [*Mirounga* spp.], Haley, Deutsch & LeBoeuf, 1994; Modig, 1996; for red deer [*Cervus elaphus*], Clutton-Brock, Albon & Guinness, 1988; for savannah baboons [*Papio cynocephalus*], Altmann, Hausfater & Altmann, 1988).

Larger males may have an advantage in combat (Taylor, Larsen & Schweinsburg, 1985; Ramsay & Stirling, 1986; Craighead *et al.*, 1995) and therefore intimidate smaller males and estrus females (*cf.* Smuts & Smuts, 1993). The ability to intimidate females could be advantageous whether a population is dispersed or aggregated, as near salmonid spawning streams or garbage dumps. In aggregations, it may be critical for males to breed soon after a female entering estrus ovulates, to enhance sperm competitiveness. Optimal timing of copulations may depend on the male's ability to dominate aggregations of both males and females rather than rely on chance opportunities at the periphery (Craighead *et al.*, 1995). In dispersed populations, size may help prolong the domination and containment of an estrus female once she is found (Hamer & Herrero, 1990). To a lesser extent, larger body size also

may facilitate use of a larger range (Garland, 1983; Fancy & White, 1985) and thereby increase frequency of encounter with reproductive females.

If lean body mass has a major positive effect on the reproductive success of male grizzly bears, there should be sex-linked traits among males that enhance lean body mass growth. These traits would be preference for dietary protein, preference for habitats where proteinaceous foods are more abundant, and efficient lean body mass accretion — especially in contrast to females. Such traits are expected because accretion of lean body mass is more efficient when an omnivore eats protein derived from muscle (Cunningham, Friend & Nicholson, 1962; McDonald, Edwards & Greenhalgh, 1988; Whittemore, Tullis & Emmans, 1988). Compared to other bear species, opportunities for sex-related differences in consumption of protein by individual grizzly bears are greater because their diets can include substantially different amounts of ungulate or rodent meat (Mattson, 1997b, 1998; Jacoby *et al.*, 1999).

The possibilities of sex-linked influences of diet protein or sex-related differences in protein consumption have hitherto received little attention in bear research. Male grizzly bears often eat more meat than do females (Boertje *et al.*, 1988; Mattson, 1997b; Jacoby *et al.*, 1999); although this result is not consistent for all studies (Ballard, Spraker & Taylor, 1981; Reynolds & Garner, 1987; Case & Buckland, 1998). There has been no investigation of sex-related differences in use of habitats that contain high concentrations of proteinaceous foods such as elk, bison, moose (*Alces alces*), or ground squirrels (*Spermophilus* spp.); or investigation of sex-related differences in efficiency of lean body mass accretion. Even so, there is ample evidence from swine and humans that, compared to females, males of these omnivorous species accrete more lean body mass on the same diet, or exhibit a greater response to supplemental protein (Davies, Pearson & Carr, 1986; Siebrits *et al.*, 1986; Campbell, Taverner & Curic, 1988; Frisch, 1990).

Several feed-back loops potentially exist that could reinforce growth in lean body mass of male grizzly bears (Fig. 1). For one, large males often have prerogative on concentrated foods that contain a high fraction of protein (Stonorov & Stokes, 1972; Egbert & Stokes, 1976; Seller & Aumiller, 1994; Craighead *et al.*, 1995). Consequently, larger males would more likely grow larger at a faster rate than competing smaller males. For another, among other omnivores large lean body mass and high levels of dietary protein

promote efficient protein digestion and lean body mass growth and maintenance (Clutton-Brock & Harvey, 1983; Campbell *et al.*, 1988; Karasov & Diamond, 1988). Consequently, initially high levels of dietary protein can lead to larger size, leading to increased rates of lean body mass growth. Especially where major protein sources are aggregated, young males deprived of protein could be at a perpetual and increasing disadvantage in future competition for high quality food and breeding opportunities. Limits to lean body mass would be imposed by increasing absolute energetic costs of maintenance coupled with difficulties in finding sufficient quantities of digestible energy-dense foods.

I derived the following research hypotheses pertaining to males from the preceding information:

- (i) male grizzly bears prefer higher-protein-content foods more than do females;
- (ii) when available, male grizzly bears eat more high-protein-content foods than do females;
- (iii) male grizzly bears use habitats containing high-protein-content foods more intensively than do females, especially during hyperphagia;
- (iv) males that eat more high-protein-content foods are larger in size and exhibit larger annual ranges compared to males that eat less proteinaceous foods;
- (v) larger males more often 'win' confrontations with smaller males;
- (vi) larger males more often copulate with females and more often at 'high quality' times compared to smaller males;
- (vii) male grizzly bears are more efficient at lean body mass accretion compared to females; and
- (viii) grizzly bears fed a high-protein diet are more efficient at lean body mass accretion compared to bears fed a low-protein diet.

Reproductive success of female grizzly bears

Although several authors have theorized about factors influencing the reproductive success of female grizzly bears (*e.g.*; Tait, 1980; Bunnell & Tait, 1981; Bunnell & Hamilton, 1983; Stringham, 1980, 1983, 1986), little has been empirically tested. Most evidence for dietary effects on female reproduction come from studies of the smaller-bodied and less mobile American black bear (*U. americanus*). Where a population had less access to fruit, either because of a poor fruit crop or because of few fruit-producing trees and shrubs, there

were fewer and smaller litters (e.g., Jonkel & Cowan, 1971; Rogers, 1987; Elowe & Dodge, 1989; Miller, 1994). This was clearest contrasting bears with greater and lesser access to high-fat-content fruits (called 'hard mast') (LeCount, 1982; Eiler, Wathen & Pelton, 1989; Clark & Smith, 1994; McLaughlin, Matula & O'Connor, 1994; McLean & Pelton, 1994). Several studies of black and grizzly bears (Schwartz & Franzmann, 1991; Reynolds & Garner, 1987; Hildebrand *et al.*, 1999) also have suggested that females who ate more ungulate or salmon meat were more fecund than females who ate less. There is good evidence that females in poorer condition — indicated by blood chemistry, smaller body size, or smaller adipose reserves — produced fewer cubs (Alt, 1989; Kolenosky, 1990; Stringham, 1990a,b; Derocher, Stirling & Andriashek, 1992; McLellan, 1994; Noyce & Garshelis, 1994; Derocher & Stirling, 1995, 1996; Hildebrand *et al.*, 1999).

This field research, as well as laboratory studies of grizzly bears and other large mammals, suggests that adipose reserves play a central role in regulating reproduction of female grizzly bears (Fig. 2). Much of cub growth during the first year is contingent on lactation by the dam (Ofstedal *et al.*, 1993; Arnould & Ramsay, 1994; Farley & Robbins, 1995). Cub survival also may be contingent on lactation (Ofstedal *et al.*, 1993; Arnould & Ramsay, 1994). In turn, lactation depends entirely on adipose reserves during the extended period of post-partum hibernation (February-April or May; Ramsay & Dunbrack, 1986; Hellgren 1998) and partly depends on these reserves during the period of higher milk production that follows emergence from the den (Derocher, Andriashek & Arnould, 1993; Farley & Robbins, 1995). Finally, some researchers have speculated that maternal adipose reserves enhance the likelihood of blastocyst implantation after the long delay (~four months) in fetal development arrested at the blastocyst stage (Rogers, 1976; Ramsay & Stirling, 1988; Tsubota *et al.*, 1990).

If adipose reserves are critical to the reproduction of female grizzly bears, then fat will be an important part of the female diet (Gilbert & Lanner, 1995). Because grizzly bears produce high-fat-content milk (Jenness, Erickson & Craighead, 1972; Farley & Robbins, 1995), post-denning lactation likely depends on fat, not just from maternal reserves, but also from the contemporary maternal diet. Dietary fat is more efficiently converted to milk fat than from any other diet nutrient (Pond, 1984; Pettigrew & Moser, 1991). The same is true for conversion to adipose reserves (Allen, 1976; McDonald *et al.*, 1988; Pettigrew & Moser,

1991). Consequently, reproductive-aged female grizzly bears are more likely than males to prefer dietary fat and seek out habitats where lipid-rich foods are abundant. Female gender, increased body fat, and increased intake of dietary fat all promote efficiency of body fat accretion, with potential self-reinforcing consequences (Schemmel, 1976; Kendall, 1984; Gross, Wang & Wunder, 1985; Pond *et al.*, 1986; Pekas, 1991).

The reproductive success of females also may be influenced by contact with other adult bears, especially males that are unrelated to a dam's offspring (Fig. 2). Adult grizzly bears kill cubs. Most often the killer is an adult male of unknown relation to the cub, although adult females also are known to kill cubs (McLellan, 1994). However, it is uncertain to what extent infanticide occurs, the extent to which it influences population dynamics, and the extent to which it is influenced by density and numbers of immigrant males (Stringham, 1980, 1983, 1986; McLellan, 1994; Swenson *et al.*, 1997). Even so, infanticide can have dramatic effects on the reproductive success of some females especially if the female is killed along with her cub (*e.g.*; Murie, 1981; Dean, Darling & Lierhaus, 1986).

If infanticide by males is common or if such infanticide has been a potent evolutionary influence, then its effects should be evident in habitat use by adult female grizzly bears. Such an effect was apparent in a study along the Rocky Mountain Front, Alberta, Canada (Wielgus & Bunnell, 1994), where females with young avoided areas primarily used by immigrant males. Other studies have documented females with cubs avoiding what were probably resident males (Pearson, 1975; Darling, 1987). Habitat segregation, between adult males on one hand and subadult males and females with young on the other, also was evident in studies of relations between grizzly bears and humans in Yellowstone National Park (Mattson *et al.*, 1987, 1992a; Reinhart & Mattson, 1990a) and southeastern British Columbia (McLellan & Shackleton, 1988).

I derived the following research hypotheses pertaining to females from the preceding information:

- (ix) female grizzly bears prefer higher-fat-content foods more than do males;
- (x) when available, female grizzly bears eat more fatty foods than do males;
- (xi) controlling for potential effects of infanticide, females that eat more dietary fat are more fecund than females that eat less;

- (xii) controlling for possible avoidance of males, female grizzly bears spend more time than males in with abundant fatty foods;
- (xiii) controlling for habitat and diet preferences, female grizzly bears accompanied by dependent young avoid habitats characteristically used by adult males, especially those unrelated to their offspring;
- (xiv) among grizzly bears, females are more efficient than males at accreting adipose reserves; and
- (xv) compared to grizzly bears fed a low-fat diet, bears fed a high-fat diet are more efficient at accreting adipose reserves.

Other theoretical considerations

I expected factors other than nutrient content, as such, to unify or differentiate diet and habitat selection among grizzly bears. The digestible energy of bear foods can vary from 10 to 95% (Mealey, 1980; Bunnell & Hamilton, 1983; Pritchard & Robbins, 1989).

However, energetic benefits are dictated by the difference between energy digested and the costs of finding and handling a food (Stephens & Krebs, 1986). All else equal, it is a basic ecological expectation that animals will select habitats and foods that provide them with the greatest net digested energy, despite debate over details of how this selection occurs. I consider net digested energy to be a function of digestibilities, bite sizes (Gross *et al.*, 1993; Mattson, 1997c; Welch *et al.*, 1997), and costs of extraction (Holcroft & Herrero, 1984; Mattson, 1997c). Consequently, I hypothesized that:

- (xvi) all grizzly bears, when foraging, select habitats and foods that provide them with the greatest net digested energy.

Foods with concentrated protein and lipids potentially yield the most net energy to bears, in addition to potentially being selected for nutrient content alone (Mattson *et al.* 1999).

Consequently, there is the potential complication of distinguishing selection by all bears for net energy content, as such, from selection by the genders for specific nutrients that might promote their fitness.

Roots are a special class of food. All else equal, roots offer a reward of constant size regardless of the size of the immediate excavation. Because the energy required to shear soil increases geometrically with the diameter of an single excavation (Hillel, 1980), bears with large paws are predictably at an energetic disadvantage digging roots compared to bears with

small paws. Whereas a large bear could regulate its' expenditure when excavating larger volumes simply by making fewer digs, such recourse would be unavailable where the total excavation was the size of an individual paw, as with digging most roots. For this reason I hypothesized that:

- (xvii) grizzly bears with large paws (i.e., adult males) excavate fewer roots compared to grizzly bears with smaller paws (i.e., subadults).

Diet composition in Yellowstone

The models presented above are a basis for expecting that, while both genders prefer habitats and foods characterized by high levels of net digested energy, the genders exhibit different dietary preferences relative to protein and fat content of foods. Also, females with young avoid habitats characteristically used by adult males. Consequently, I expected that consumption of different foods by Yellowstone grizzly bears would be affected by gender and the parturient status of females (Fig. 3). I also expected that consumption of different foods would be affected by size of the bear and its range.

Meat from elk (*Cervus elaphus nelsoni*) and bison (*Bos bison*) and seeds of whitebark pine (*Pinus albicaulis*) trees are potentially the most important sources of energy and nutrients for Yellowstone's grizzly bears (Mattson *et al.*, 1991a; Mattson & Reinhart, 1994; Mattson, 1997c; Mattson *et al.*, 1999). The seeds of whitebark pine are rich in fats (Lanner & Gilbert, 1994) while meat is a rich source of digestible protein. Unlike most other grizzly bears in North America, Yellowstone bears do not eat many fleshy fruits. Roots of yampah (*Perideridia gairdneri*) and biscuitroot (*Lomatium cous*) are the primary sources of digestible carbohydrate, in the form of starch rather than simple sugars (Mattson *et al.*, 1991a; Mattson *et al.*, 1999).

Some high-quality foods are locally important. Since 1986, fat-rich army cutworm moths (*Euxoa auxiliaris*) aggregated in alpine rock fields have been heavily used by bears in the eastern part of the Yellowstone ecosystem (Mattson *et al.* 1991b; French, French & Knight, 1994). Consumption of protein-rich spawning cutthroat trout (*Oncorhynchus clarki*) by bears has increased since the mid-1970's (Reinhart & Mattson, 1990a) and is localized in south-central Yellowstone National Park (Mattson & Reinhart, 1995). Foods that contain substantial amounts of fiber (graminoid and forb foliage) or chitinous protein (adult ants and hornets, Formicidae and Vespidae) are little digested by grizzly bears (Pritchard & Robbins,

1989) and are consequently not an important source of energy anywhere in the region (Mattson *et al.*, 1999).

The abundance of important bear foods varies substantially with time-of-year in Yellowstone. Carcasses of ungulates are most common on ungulate winter ranges March through mid-May (Green *et al.*, 1997). During May and June, the foliage of herbaceous vegetation contains maximum fractions of protein and minimum fractions of fiber (Mattson *et al.*, 1999) – conditions that allow greater digestion (Pritchard & Robbins, 1989) and promote peak use of foliage by grizzly bears during these months (Mattson *et al.*, 1991a). This time of year also coincides with peak mating activity among Yellowstone's grizzly bears (Craighead *et al.*, 1995). By July, starch content of roots is high and excavations of this food by grizzlies become more common (Mattson, 1997c; Mattson *et al.*, 1999). Heavy feeding (hyperphagia) begins about mid-July (Mattson *et al.*, 1991a; Mattson, 1997a). If whitebark pine seed crops are large, consumption of this food can dominate grizzly bear activity after cones mature in mid to late August (Kendall, 1983; Mattson & Reinhart, 1994, 1997). Cones are excavated from red squirrel (*Tamiasciurus hudsonicus*) middens, where the otherwise indehiscent cones are cached by squirrels.

Abundance and consumption of important grizzly bear foods can dramatically change among years (Mattson *et al.*, 1991a). Whitebark pine cone crops at permanently-marked transects varied from one to 48 cones tree⁻¹, 1980–92 (Knight, Blanchard & Mattson, 1993). Consumption of pine seeds by grizzly bears correspondingly varied, but in an abrupt way relative to availability resembling a step function (Mattson & Reinhart, 1994). Consumption was negligible when crops were small, but increased dramatically when cone crops exceeded 20–24 cones tree⁻¹ on permanently-marked transects (*cf.*, Kendall, 1983) in the Yellowstone ecosystem. Numbers of ungulate carcasses on ungulate winter ranges were equally variable among years and use by bears exhibited a similar threshold relationship to availability (Green *et al.*, 1997; Mattson, 1997b).

Finally, there also was geographic variation across Yellowstone's grizzly bear range in numbers of ungulates and cone-producing whitebark pine trees and the extent of non-forest areas containing root foods. Elk and bison were densest in the northern part of the ecosystem (Mattson, 1997b). Whitebark pine was most abundant to the north and east (Despain, 1990). High-quality foods of any type were least common in southwestern parts of grizzly bear

range as was non-forest habitats supporting root and foliage foods (Despain, 1990). This geographic variation in abundance and types of foods was likely expressed in range sizes, being larger where food was less abundant or occurred as dispersed aggregations (Canfield & Harting, 1987).

I used the preceding information together with the model in Figure 3 to derive the following research hypotheses specific to grizzly bears in Yellowstone:

- (xviii) whitebark pine seeds are more often used by females than by males;
- (xix) ungulates are more often used by males than by females;
- (xx) females that consume more roots and foliage produce fewer cubs than females that consume more pine seeds; and
- (xxi) grizzly bears consume different foods dependent on the abundance of each by year, season, and area, and variation in abundance of high-quality foods.

The theoretical models in Figures 1–3 imply other hypotheses, including ones related to the effects of multiple paternity and aggregation of foods. The hypotheses I present above are germane to the topic of this dissertation. The Yellowstone grizzly bear field study, 1977–92, provided information that I used to evaluate hypotheses (ii)–(iv), (x)–(xiii), and (xvi)–(xxi). I view the remaining hypotheses as impetus for future laboratory studies of bear diet and growth or future studies of grizzly bear behavior at aggregations.

Study area

The ~23,000 km² study area corresponded to the known range of Yellowstone's grizzly bear population, extending south-north from 43°30' to 45°15'N latitude and east-west from 109°30' to 111°30'W longitude. Most of the area occupied by grizzly bears was >2,760 m a.s.l., and is comprised of remote mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Annual temperatures averaged about 0°C. Precipitation substantially varied in amount and timing with elevation and geographic location, being drier to the north and east and exhibiting an April-June peak to the north and an October-February peak to the south (Dirks & Martner, 1982; Despain, 1987). The majority of precipitation fell as snow, with winter accumulations reaching 20-260 cm before melting during March-June, depending primarily on elevation and latitude.

Most (~75%) of the study area was forested and most of this forest was dominated by lodgepole pine (*Pinus contorta*; Despain, 1990). Whitebark pine was abundant only above 3,300 m elevation. Alpine areas were most common in the eastern one-third of the study area, above 4,000 m. Other non-forested areas consisted of wet meadows at mid-elevations and, particularly in the northern one-quarter of the study area, of extensive low-elevation (<2,800 m) grass- and shrublands characterized by Idaho fescue (*Festuca idahoensis*), mountain sagebrush (*Artemisia tridentata vaseyana*), and bluebunch wheatgrass (*Agropyron spicatum*). Forest structure considerably varied during the study primarily due to mortality of trees caused by fire and epidemic populations of mountain pine beetle (*Dendroctonus ponderosae*; Despain, 1990). The largest fire occurred in 1988 and burned approximately 560,000 ha.

Ungulates were abundant in most of the study area. About 45,000 elk and 2,000 bison occurred in or near Yellowstone National Park (Singer, 1991). Mule deer (*Odocoileus hemionus*) and moose also were common, at lower and higher elevations, respectively. Knight & Eberhardt (1985), Mattson *et al.* (1991a,b), Blanchard & Knight (1991), Craighead *et al.* (1995), and Green *et al.* (1997) describe aspects of the study area in greater detail.

Methods

Field methods

Trapping, measurement, and relocation

Grizzly bears were trapped, marked, and radio-relocated according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). In common with other studies of this nature, efforts were made to trap representatively (by area and less so by sex and age), but differences among animals in susceptibility to capture combined with administrative and logistical constraints on access precluded a random sample. All radiorelocations used in this analysis were made from fixed-wing aircraft and recorded by their universal transverse mercator (UTM) coordinates. Methods for measuring trapped bears are described by Blanchard (1987). Weights were obtained from spring scales or were estimated by experienced field personnel. Seven body and four foot measurements were obtained using a steel tape.

Site features and activities of grizzly bears at telemetry relocations

Field crews visited and described a portion of the aerial-telemetry locations. Choice of locations was not random, primarily because of logistical constraints. Most of the study area was without roads, and use of helicopters was either administratively prohibited or prohibitively expensive. Ground sampling consequently emphasized equal representation of different bears and different areas (see below), as well as visits to as many telemetry locations as possible. Each visited location was described according to protocols reported by Mattson (1991).

Field crews located variable-radius forest inventory plots at the center of grizzly bear activity, or in the absence of bear sign, at a randomly selected distance (≤ 10 m) and direction from the recorded radiotelemetry UTM. All trees in the plot were identified by species, whether dead or alive, and the diameter of each was measured at 1.4 m aboveground. Additional information on vegetation structure was recorded within about 10 m of plot center — in a 314-m² area. This information included three indices and one measure of coarse woody debris (amt [1–7, sparse to heavy], size [1–7, small to large], decomposition [1–6, solid to well-decomposed], and % cover), Fischer's (1981) classification of the size and volume of woody debris, and estimated percent cover of forbs, graminoids, shrubs, and overstory trees (>1.4 m-tall). I worked closely with all field personnel who used these

subjective descriptors from 1984 to 1992, and was able to standardize their application (i.e., achieve consistent convergence of estimates) through regular field exercises. Estimates of the current-year's standing crop of graminoids were based on double-sampling (Mattson, 1997a). Aggregate dimensions (average ht [*HT*] in cm and estimated % cover [*CVR*]) were measured prior to clipping, oven-drying, and weighing graminoids from 10 to 15 systematically-placed 10-dm² microplots (Merrill *et al.*, 1993). Biomass (g; *BM*) was related to *HT* and *CVR*: $\ln BM = 1.042 \ln(HGT \times CVR)$ ($r^2 = 0.98$; Mattson, 1997a).

Field crews described all grizzly bear sign found at ground-sampled telemetry locations. Sign that was spatially contiguous — often part of what appeared to be a single foraging bout — was included in these descriptions and ascribed to a specific location if the sign was within about 200 m of the specified UTM coordinates. Where roots were dug, individual digs were censused or estimated from systematically placed plots (Mattson, 1997c). Excavations in logs and hills for ants were measured, including average diameter of the log where it was torn by the bear, total tear length, and average tear width as a percent of total log circumference. Total excavated volume was estimated from these dimensions and from similar dimensions of excavated ant hills as the product of length \times percent circumference \times cross-sectional area (Elmork & Unander, 1998). Volumes excavated in red squirrel middens for whitebark pine seeds were similarly estimated, and the total number of observable excavated cones was counted (Mattson & Reinhart, 1997). I used standardized tables of edible dry weight for species, sex, and age-classes of ungulate (Mattson, 1997b) to estimate the total biomass available to bears from carcasses found at telemetry locations. I calculated ingested biomass calculated as the product of edible carcass biomass \times the proportion of each carcass that was estimated to have been eaten by bears (Mattson, 1997b). Grazing was rated as light, moderate, or heavy based upon direct evidence (cropping of the appropriate age, associated with bear tracks), the number of individual tracks and beds at a site, and the number and content of associated feces (i.e., whether foliage was found in the scat comparable to that present at the site) (Mattson, 1997a).

Nutrient content of bear foods

Field crews collected samples of foods consumed by bears at most sites where evidence of feeding was observed, 1987–92. Inconsistencies in this sampling resulted from limited availability of funds for laboratory analysis during some years and from

circumstances associated with sampling remote sites. Samples were restricted to vegetal foods, including foliage of graminoids, forbs, and horsetail (*Equisetum* spp.), root caches made by pocket gophers (*Thomomys talpoides*), and the roots of excavated species. Samples of plant parts used by bears — usually 10–500 g of foliage or 10–30 individual roots — were as similar to what the bears ate as possible (*cf.* Mattson, 1997c). Samples were oven-dried at 40°C to a constant weight.

All samples were analyzed for crude protein (by Kjeldahl Nitrogen), crude fiber (CF), and ash content by standard (Weende) proximate analysis. Roots were analyzed for starch content by a method developed at the Chemistry Station Analytical Laboratory of Montana State University (Mattson, 1997c). A double-sample ($n = 48$) of foliage and roots was analyzed for both CF and total dietary fiber (TDF; Prosky *et al.*, 1984) content during 1989–90. This facilitated application of the work by Pritchard & Robbins (1989) that relied on TDF to investigate digestive efficiencies of grizzly bears. CF was related to TDF: $\text{logitCF} = -1.36 + 0.97\text{logitTDF}$ ($r^2 = 0.84$; $\text{df} = 1 / 46$; $F = 244.2$; $P < 0.001$).

Analysis methods and considerations

Sampling units and independence

By the standards of philosophy, an optimal sampling unit “...cannot be further subdivided into classes relevant to the occurrence of a phenomenon of interest” (Salmon, 1984). A finely resolved sampling unit is desirable for other reasons. Such a unit allows for greater precision (Yates, 1953). Finer resolution also guards against specification error that becomes more likely if units constitute aggregations of elements that are more directly relevant to a research hypothesis (Langbein & Lichtman, 1978). For example, if the behavior exhibited by bears at given spatial and temporal coordinates is of interest, aggregating to the individual bear over some greater area and period of time increases the chance that the effects of some covariate will be masked and that parameter estimates will be correspondingly biased. By these standards, where the research hypothesis was related to the probability of a certain outcome at a given time and place, the sample unit corresponded to a telemetry location. This unambiguously held for analyzing the likelihood that a specific behavior was exhibited by a bear at a given location as a function of covariates including time-of-year, year, area, class-of-bear, and site features. Where the research hypothesis related to range or

body size, the individual animal constituted the smallest relevant class and thereby constituted the sampling unit.

Individual sample units may or may not be statistically independent; rarely can biological independence be expected. This holds for individual telemetry locations as well as individual animals. Independence (formally, $p[y,x] = p[y]p[x]$) implies that the state of x (one animal or location) does not influence the state of y (another animal or location) and is a necessary condition for confidence in statistical induction. Optimally, x and y are independent random variables. Kyburg (1969) usefully observes that the application of statistical knowledge "...is often simply the problem of finding the appropriate reference class, that is, the class [to] which a certain object is, relative to our body of knowledge, a random member"; meaning that, in the end, there are no substantive effects by undisclosed covariates. This idea is implicit to conditional independence and "strongly ignorable treatment effects" (Dawid, 1979; Rosenbaum, 1984).

Conditional independence exists when two random variables (x and y) are independent of each other, conditional on adjustments by a vector of covariates (z) (formally, $p[y,x|z] = p[y|z]p[x|z]$; Dawid, 1979). Individual observations can thus be 'independent' given adequate adjustments by a statistical model — a condition sufficient for valid statistical inference. The concept of conditional independence is readily extended to observational studies that do not have identifiable 'treatments' or randomization (von Mises, 1957; Kyburg, 1969; Dawid, 1979; Holland, 1986). I used conditional independence as the basis for statistical inference in this study. Conditional independence depends on the specification of covariates sufficient for statistical explanation and is the reason, along with the exigencies of relevance, why I devote much of this dissertation to the articulation of theoretical models of causal mechanisms (*cf.*, Rosenbaum, 1984).

Model selection

I emphasized the identification of statistical models that were plausible, relevant, and informative in this analysis. Plausibility and relevance are important philosophical criteria for judging theories and models, although their application in practice is non-rigorous (Salmon, 1970, 1984; Laudan, 1977; Boyd, 1985; Shrader-Frechette & McCoy, 1993; Putnam, 1995). I used statistical methods systematically to select models and estimate parameters according to standards of likelihood and information theory (Edwards, 1972;

Burnham & Anderson, 1998). Accordingly, I used the sample-size-adjusted version of Akaike's Information criterion (AIC_c ; Burnham & Anderson, 1998) as primary metric for model selection. Compared to unadjusted versions of AIC, AIC_c guards against over-fitting models at small sample sizes. AIC-type criteria derive from information theory and optimize model selection relative to bias and precision to achieve maximum accuracy (Burnham & Anderson, 1998). Bias is reduced by adding more independent variables. Precision is increased by minimizing the same. I used change-in-AIC (Δ) associated with deleting each independent variable, in turn, to judge the relative 'importance' of each term (Burnham & Anderson, 1998). I de-emphasized statistical hypothesis testing for reasons well articulated elsewhere (e.g., Yoccoz, 1991; Johnson, 1999); I used and present *P*-values solely as confirmatory information.

I specified models of grizzly bear activity at radiotelemetry locations in terms of explanatory factors likely to be operational at broad temporal and spatial scales ("distal" factors) and at the scale of the immediate site (314 m²; "proximal" factors). I first specified models comprised of distal factors (e.g., proportional area of certain vegetation types or ecosystem-averaged monthly precipitation [ppt]) and then competed these models against other models containing proximal factors (e.g., local abundance of the target food plant or measures of forest structure). The "best" model included proximal as well as distal effects. I identified models comprised solely of distal factors because many management issues (e.g., implications of changing the extent of vegetation types due to management or global climate change) are expressed at broad scales, and therefore best addressed by factors operational at that scale. Some level of choice by bears also is likely to occur at broad scales; i.e., a bear may or may not choose to be at specific place at a specific time engendering certain feeding opportunities because of coarse vegetation and weather patterns. Conversely, a bear may choose to engage in an activity solely based on proximal conditions. The presence of distal factors in "best" models therefore implies choice by bears sensitive to broad-scale features of their environment. The presence of proximal factors implies choice sensitive to features more immediate.

This approach approximates Johnson's (1980) concept of hierarchical habitat selection and follows Salmon's (1970, 1984) philosophy of statistical explanation and relevance. According to this philosophy, factors that are nearer in time and space to the event

of interest are potential candidates for “screening out” the effects of factors that are more distal, but only if the more proximal factors engender more information. All factors are recognized as surrogates or, more precisely, simply as phenomena measured nearer or farther away in space and prior time to the event of interest. “Causation” is not invoked, only statistical relevance and explanation. Causal explanation is derived from combining biological theory and statistical models (Eberhardt & Thomas, 1991).

Derived response variables

Home range size and movements. — I used smoothed adaptive kernels to estimate home range area as 50 and 95% of the theoretical total (Kie, Bladwin & Evans, 1994). Fixed kernel estimators are potentially the least biased of any available for most distributions (Worton, 1995; Seaman *et al.*, 1999). However, my concern was not with bias relative to “true” range size, but rather with comparative bias; i.e., systematic changes relative to potential explanatory variables. Fifty-percent home range estimates were less likely to be affected by sample size and extreme locations, especially in contrast to 95% estimates (Anderson, 1982). Also, they approached the maximum extent of most core areas (typically 20-35% of total range; Samuel, Pierce & Garton, 1985).

I estimated home ranges for bears with as few as 15 locations. Worton (1987) and Seaman *et al.* (1999) recommend that a minimum of 30 locations be used to estimate individual ranges. However, there is a strong tendency for area to increase even at much larger values of n (Gautestad & Mysterud, 1993, 1995; Gautestad, Mysterud & Pelton, 1998). I therefore included $\log(n)$ as a covariate to control for the effects of sample size at all levels of n (Samuel *et al.*, 1985; Gautestad & Mysterud, 1993; Hansteen, Andreassen & Ims, 1997).

I used all locations attributed to an individual bear, regardless of season and year, to estimate the size of its range provided that the locations were part of an unbroken sequence of natural movement. All locations but one obtained at a den site and all locations associated with management translocations were excluded (Blanchard & Knight 1991). Separate ranges were estimated for a bear if a non-denning-season sequence of locations was interrupted by >2 months. Under these circumstances, I calculated a sample-size weighted average of range sizes for the bear. I used regression analysis to estimate and control the effects of season and type-of-bear on range size (see below).

I also calculated harmonic mean distance between successive locations for each bear (Blanchard & Knight, 1991). Such a measure provides additional information on magnitude of movements and is relatively insensitive to n (Swihart & Slade, 1985). I averaged mean distances, weighted by n , for individual bears when there were several intervals defined either by breaks in monitoring (e.g., an interval between collar loss and recollaring) or lapses in movement due to denning (the interval between entering and leaving a den). Similar to estimates of home range size, I used management translocations and lapses of monitoring >1 month long to define the end and beginning of intervals.

Corpulence. — Field crews rarely measured body condition of bears during this study, either by blood profile or some measure of body fat. Yet, condition is important to addressing some of the research hypotheses. Although body mass has been associated with the condition or reproductive success of bears elsewhere, among grizzly bears in Yellowstone body mass may be less closely associated with condition because bears here potentially eat a diet of quite varied nutritional composition. Kingsley, Nagy & Reynolds (1988) devised an index of 'corpulence' that was the ratio of body mass to length. The basic idea was to relate measures of total body volume to measures that more closely reflect lean body volume and, assuming that 'corpulence' was correlated with adipose reserves, use the ratio or residual as an indicator of condition.

I developed and tested indices of corpulence similar to the index developed by Kingsley *et al.* (1988). However, I used more body measurements than they did and residuals rather than ratios. I indicated total body volume (in dm^3) by the product of zoological body length (tip of nose to tip of tail) times the average of cross-sectional neck area and cross-sectional chest area (Fig. 4): $BV = \text{body length} \times (([\text{neck circumference}]^2 / 4\pi) + ([\text{chest circumference}]^2 / 4\pi)) / 2$. I indicated lean body volume by the first principle component (LV) derived from the covariance matrix of measurements thought to more closely reflect non-fat body volume: front foot width and length, rear foot width and length, and head basocranial length and zygomatic width (*cf.* Blanchard, 1987; Cattet, 1990; Fig. 4). For conceptual reasons, I cubed LV after adding a constant (7) to make all values positive. I used residuals of the regression of BV on LV^3 ($r^2 = 0.71$) as an index of corpulence based on body volume (CRP_{BV}). I used residuals of a similar regression of scale weight (in kg) on LV^3

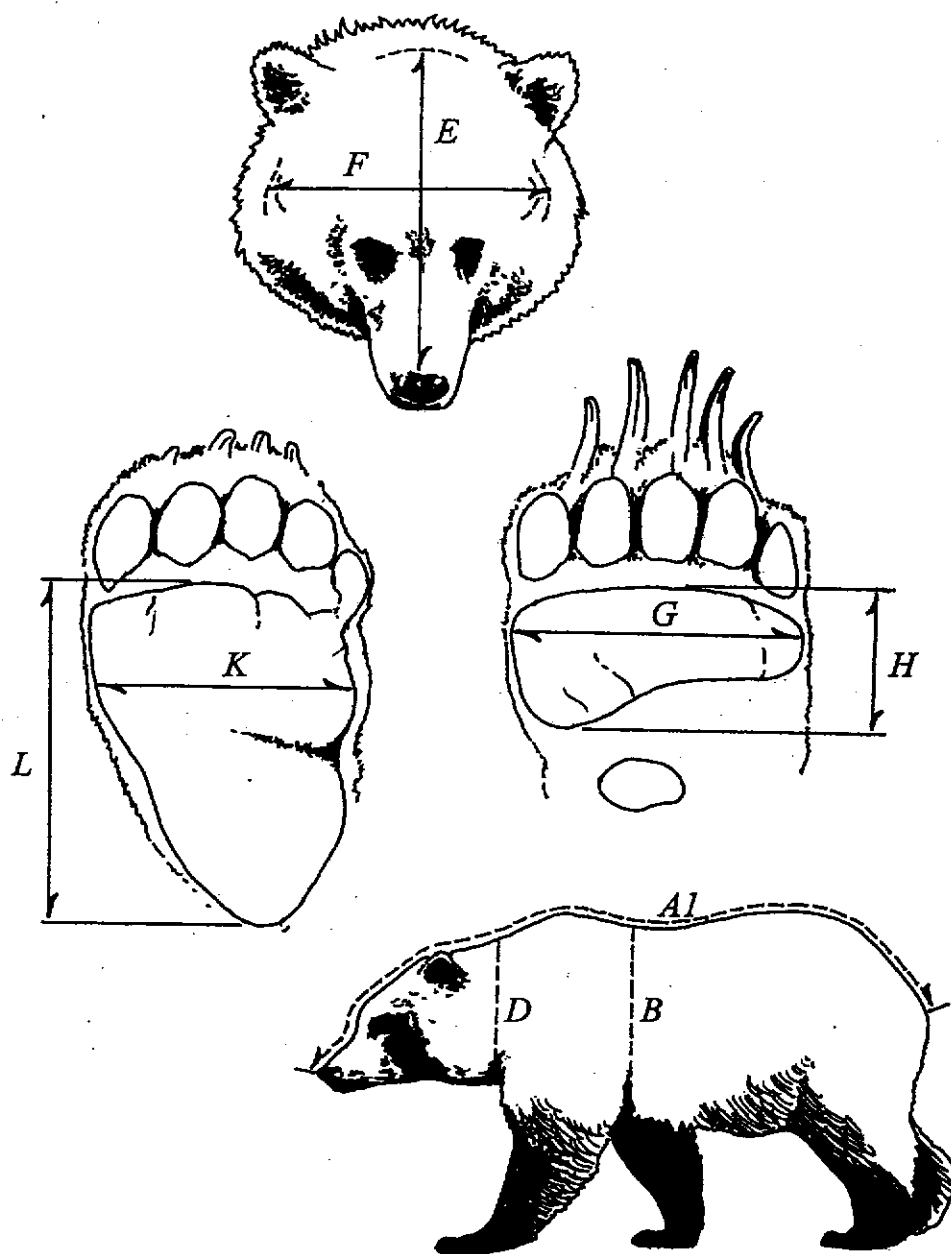


FIG. 4. Measurements used to calculate morphometric indices for Yellowstone's grizzly bears: *AI* = contour body length; *B* = chest girth; *D* = neck girth; *E* = head zygomatic width; *F* = head basocranial length; *G* = front pad width; *H* = front pad length; *K* = rear pad width; and *L* = rear pad length.

($r^2 = 0.87$) as an index of corpulence based on weight (CRP_{sw}). I square-root transformed all variables to linearize relations and homogenize variances. Males and females were pooled.

I evaluated the two indices of corpulence by correlation with estimates of total body fat using data from grizzly bears marked during a study in Kluane National Park, Yukon, Canada (McCann, 1998). These bears were measured and weighed by the same methods used during this study, except that feet were not measured. Body fat was estimated by electrical bioimpedance analysis, as described by Farley & Robbins (1994). I calculated indices of corpulence based on weights and body volume as described above except that LV was based only on head dimensions.

Lean body volume. — Measures of corpulence allowed me to partition out and examine relations with that part of body size assumed to be associated with adipose reserves. Following this logic, the index of lean body volume (LV^3) partitioned out that part of body size assumed to be more closely associated with muscle and skeletal dimensions (Cattet, 1990). However, lean body size predictably increases with age and is probably linked to gender. Because I was interested in the effects of diet and movements, the effects of age and gender needed to be controlled. The residuals of such statistical control would theoretically more closely correspond to that part of lean mass varying with diet, recognizing that the effects of gender on diet preference and the effects of gender on the efficiency of lean body mass accretion are not readily distinguished.

I used residuals to size (LV^3) expected by a fitted von Bertalanffy growth equation (von Bertalanffy, 1938) as an index to relative lean body volume (LBV). The von Bertalanffy equation takes the form: $LV^3 = ALV \times (1 - e^{-R \times (AGE - ADJ)})^3$, where ALV is asymptotic volume, R is the age-specific rate of approach to ALV , and ADJ adjusts the y axis intercept with the x (age) axis. I calculated residuals from equations fit separately for males and females. I also evaluated the linear effects of Julian date and senescence (as an additional age term) on R . The ease with which this could be done in context of the von Bertalanffy equation led me to choose this model over the more flexible Richards model of growth. Regardless, the expected penalty in bias and goodness-of-fit by adopting the von Bertalanffy over the Richards equation was predictably small (Leberg *et al.*, 1989).

Reproduction of females. — I reckoned reproductive response in two ways. In the first method I treated each annual observation of a female as a unit of analysis; i.e., for each

year and each female there was a record of whether the female was initially accompanied by 0, 1, 2, or 3 cubs-of-the-year (COY). Another entry recorded whether any of the observed cubs were subsequently lost (known or suspected) during their first year. I modeled four aspects of these responses: (1) the likelihood that a female was accompanied by COY; (2) the likelihood, given a litter, that only 1 cub was observed; (3) the likelihood, given a litter, that 3 cubs were observed; and (4) the likelihood, given a litter, that one or more cubs were lost. This approach used all available data rather than just observations of females that had been monitored for extended periods of time. Consequently, it was not as biased as conventional approaches towards females that survived or were vulnerable to repeat captures.

In the second method, I merely summed the total number of COY observed, as well as the total number of cubs lost, during the time that a female was monitored. Individual females were the implicit unit of analysis. I only used females for which I had estimates of proportional activity (see below). I modeled total cub production and total cub loss. Because numbers of cubs born and lost increased with passage of time, I included number of years that a female was monitored as a covariate. The parameter for this variable was annual COY production or loss. This approach allowed for an explicit individual-based connection between estimated diet and estimated reproductive success.

Both approaches likely underestimated cub loss and production. Both litters and losses stand a chance of being overlooked (Pease & Mattson, 1999). These issues were of little import to this analysis because I was not interested in unbiased estimates of reproductive rate, *per se*. Rather, I was interested in the effects on reproduction by factors such as female age and diet. Systematic differences in the probability of detecting cub loss or production with respect to explanatory factors was of greater concern to me because such differences would lead to models and estimates that were biased with respect to the research hypotheses.

Derived or distal independent variables

Class variables. — I classified individual bears according to gender, age, and parturient status. Subadult bears were independent of their mother and, if without cubs, <5 years old. Adult bears were either with cubs or ≥ 5 years old (Erickson *et al.*, 1968; Craighead *et al.*, 1995; White *et al.*, 1998). I further distinguished adult females on an annual basis by whether they accompanied COY or accompanied older offspring during $\geq 50\%$ of the

active season. Otherwise, I classified adult females as 'alone'. Where individual telemetry locations were units of analysis, I denoted bears classes by a categorical variable. Where individual bears were units of analysis, I denoted bear classes by separate variables with each enumerating the proportion of total locations from the bear of interest obtained while the bear was in the corresponding class.

I reckoned feeding activity by nine categories (Fig. 5) defined by similarity of six per g characteristics of the ingested foods: digested energy, indexed expended energy, % protein, % fat, % starch and sugar, and % crude fiber (Mattson *et al.*, 1999). I used average linkage cluster analysis initially to define 14 diet categories based on the six food characteristics. I subsequently consolidated five of the categories with others that were next most similar because there were too few observations (<20) of the associated feeding activity at radiotelemetry locations to support estimation. I added two categories ('bedded' and 'no feeding sign') to the 9 associated with feeding, for a total of 11, to cover the full spectrum of bear activities (Table 1). I represented each of these categories by a separate variable that enumerated the corresponding proportion of total activity for the bear of interest.

Yellowstone's grizzly bear range was classified and mapped by land management agencies according to features of the site and vegetation and whether in or out of various types of ungulate winter ranges (Mattson *et al.*, 1999). Site and vegetation features were denoted by habitat and cover types. Habitat type reflects the invariate potential or features of a site (Mueggler & Stewart, 1980; Steele *et al.*, 1983) while cover type reflects existing structure of the vegetation (Despain, 1990). Thousands of habitat and cover type combinations exist. I reduced these combinations to 12 for this analysis based primarily on similarity of grizzly bear activity and secondarily on similarity of biophysical features (Mattson *et al.*, 1999; Tables 2 & 3). I additionally described habitats in terms of 3 types of ungulate winter ranges (low-elevation elk, high-elevation elk, and bison; Mattson *et al.*, [1999]).

I denoted each habitat and winter range type for analysis by a separate variable. The values of each of these variables associated with a given bear location were determined by the Bear Management Unit (BMU) containing the location, and corresponded to the proportion of the BMU in each habitat or winter range type. I assigned proportions before and after the fires of 1988 to bear locations depending on whether the location was obtained

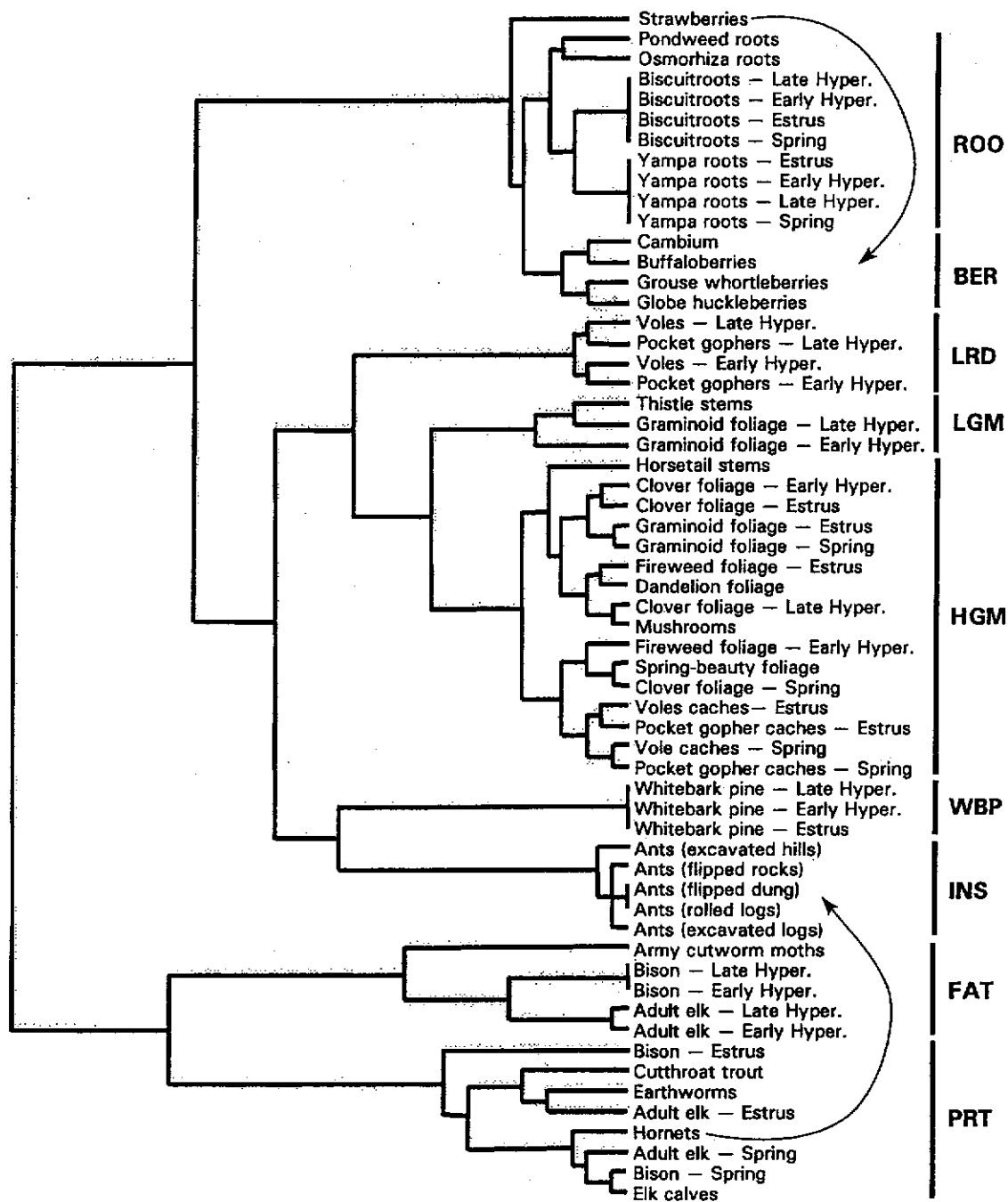


FIG. 5. Clustering of Yellowstone grizzly bear foods based on energetic and nutritional characteristics. Aggregate types used in analysis of relations between activity and movements, morphology, and reproduction of bears are denoted by bolded acronyms and vertical lines. As indicated by the arrows, strawberries and hornets were reallocated to types based on taxonomic or structural relations. Spring, Estrus, and Hyper.(Hyperphagia) refer to seasons defined in the text.

TABLE 1. Description of activity types used in the analysis of relations between activities of individual bears and their movements, morphological characteristics, and reproduction, for Yellowstone grizzly bears, 1977-92.

Activity type	Description	Energetic and nutritional characteristics of associated foods†					
		Digested energy (KJ g ⁻¹)	Expended energy (index, g ⁻¹)	crude protein (%)	ether extract (%)	starch or simple sugars (%)	crude fiber (%)
Use of whitebark pine seeds (WBP)	Scavenging of fallen cones or excavation of cones from red squirrel middens	11.4	1.1	12.8	27.1	0	34.8
Use of high-protein foods (PRT)	Fishing for cutthroat trout, scavenging of winter-killed ungulates, scavenging and predation on ungulates during Estrus, and excavation of earthworms	17.4	1.9	72.2	16.3	0	0
Use of high-fat foods (FAT)	Scavenging and predation on ungulates during Hyperphagia and excavation of army cutworm moths from talus	22.8	2.0	46.1	51.2	0	0
Use of roots (ROO)	Excavation of roots	10.7	1.4	6.1	1.3	32.8	8.4
Use of Hymenoptera (INS)	Excavation of ants and hornets from logs, dirt and debris hills, and ground nests	13.3	8.3	43.9	29.1	0	15.3
Use of rodents, Hyperphagia (LRD)	Excavation of pocket gophers, voles, or their food caches during Hyperphagia	10.8	4.4	41.4	6.6	2.3	5.0
Use of berries (BER)	Browsing of berries, all species	11.0	0.6	7.5	3.0	34.5	0
Use of high-quality vegetal foods (HGM)	Grazing of forbs other than thistle year-round and graminoids during Spring and Estrus; excavation of pocket gophers and their food caches during Spring and Estrus; and excavation of mushrooms	7.7	0.7	20.3	0.7	1.0	14.4
Use of fibrous foods (LGM)	Grazing of elk thistles year-round and grazing of graminoids during Hyperphagia	2.8	0.2	9.4	0	0	29.5
Bedded	Sign of bedding	—	—	—	—	—	—
No feeding sign	No sign of bedding or feeding; tracks, feces, or other sign may be present	—	—	—	—	—	—

†For details on energetic and nutritional characteristics of food used by Yellowstone's grizzly bears and associated methods, see Mattson *et al.* (1999).

TABLE 2. Description of habitat and winter range types used to map grizzly bear habitat in the Yellowstone area and used to analyze patterns of activities by Yellowstone's grizzly bears. These types were defined on the basis of similarity of grizzly bear activities and similarity of site and vegetation features. Methods for derivation are described by Mattson *et al.* (1999).

Habitat type acronym	Description
Nonforest types	
DRYMD	Dry meadows and grasslands; typified by <i>Agropyron spicatum</i>
LITHC	Rocky convex ridges; tundra; typified by <i>Festuca idahoensis</i> & <i>Poa alpina</i>
MESMD	Mesic meadows and grasslands; typified by <i>Geranium viscosissimum</i> , <i>Phleum alpinum</i> , and <i>Agropyron caninum</i>
TALUS	Talus, cliff, and other rock; largely unvegetated
WETMD	Marshes, fens, and wet meadows; typified by <i>Carex</i> spp., <i>Deschampsia cespitosa</i> , & <i>Calamagrostis canadensis</i>
Forest types	
DOPEN	Dry sites recently deforested by timber harvest or fire
HABLA	High-elevation subalpine fir climax sites; typified by <i>Arnica</i> spp. and <i>Juniperus communis</i>
HPIAL	High-elevation forested sites with mature whitebark pine
HPSME	High-elevation Douglas-fir climax sites; typified by <i>Arnica cordifolia</i> , <i>Berberis repens</i> , <i>Juniperus communis</i> , and <i>Symphoricarpos oreophilus</i>
HVASC	High-elevation sites with grouse whortleberry-dominated ground layer
LPICO	Low-elevation lodgepole pine-dominated sites; typified by <i>Carex geyeri</i> , <i>C. rossii</i> , <i>Calamagrostis rubescens</i> , & <i>Purshia tridentata</i>
MOPEN	Mesic-wet sites recently deforested by timber harvest or fire
LPIEN	Low-elevation Engelmann spruce-dominated sites; typified by <i>Calamagrostis canadensis</i> , <i>Equisetum arvense</i> , & <i>Galium trifolium</i>
MABLA	Mesic-wet subalpine fir climax sites; typified by <i>Thalictrum occidentale</i> & <i>Osmorhiza chilensis</i>
MPSME	Mesic Douglas-fir climax sites; typified by <i>Symphoricarpos albus</i> , <i>Spirea betulifolia</i> , & <i>Calamagrostis rubescens</i>
Ungulate Winter ranges	
BIS	Bison winter range
EHE	High-elevation elk winter range
ELE	Low-elevation elk winter range

TABLE 3. Percent occurrence of different activities by habitat type, for radio-marked Yellowstone grizzly bears, 1977-92. Activity types are described in Table 1. Habitat types are described by Mattson *et al.* (1999). The first value of each entry denotes the percent occurrence of the corresponding activity, by habitat type. The second value, separated by a '/' from the first, denotes the percent of all activity within a habitat type that was of the corresponding type of activity. Bolded values denote either a high percentage (>10) of the corresponding activity occurring in the habitat type or a high percentage (>7) of the total activity within a habitat type being of the corresponding activity type.

Habitat type	Type of activity																NO SIGN
	WBP	UNG	PEGA	LOCO	OSCH	ANT (LOG)	ANT (HILL)	MOTH	GRAM	TAOF	TRFL	CISC	MUSH	RDNT	BER	BED	
Nonforest																	
DRYMD	0/0	5/4	17/8	20/14	0/0	1/1	14/3	0/0	11/7	0/0	0/0	0/0	0/0	16/8	7/1	0/0	7/54
LITHC	0/0	0/0	2/1	71/66	0/0	0/0	5/1	100/13	4/4	6/1	8/1	0/0	0/0	0/0	0/0	2/3	1/10
MESMD	0/0	9/5	59/25	1/1	0/0	4/6	41/7	0/0	16/9	28/4	17/2	67/5	0/0	45/20	0/0	0/0	2/12
WETMD	0/0	6/7	6/4	0/0	0/0	1/3	0/0	0/0	17/19	0/0	50/9	33/4	0/0	14/11	0/0	1/1	2/29
Forest																	
DOPEN	0/0	4/3	0/0	4/3	0/0	4/8	5/1	0/0	15/11	0/0	0/0	0/0	0/0	3/2	0/0	6/7	7/59
HABLA	5/6	4/2	0/0	0/0	0/0	7/10	9/2	0/0	4/2	0/0	0/0	0/0	4/1	2/1	7/1	9/8	9/62
HPIAL	79/43	0/0	0/0	4/1	7/1	12/8	0/0	0/0	3/1	0/0	0/0	0/0	17/1	2/1	27/1	14/6	12/35
HVASC	8/6	12/5	0/0	0/0	0/0	11/10	5/1	0/0	0/0	6/1	0/0	0/0	26/3	0/0	20/1	16/9	16/61
LPICO	1/1	20/11	2/1	0/0	4/1	10/13	0/0	0/0	1/1	0/0	0/0	0/0	52/8	0/0	0/0	17/13	9/48
MOPEN	0/0	5/3	9/4	0/0	4/1	6/9	9/2	0/0	17/10	56/8	8/1	0/0	0/0	10/5	0/0	9/8	7/42
LPIEN	0/0	7/8	0/0	0/0	0/0	5/13	0/0	0/0	0/0	0/0	8/1	0/0	0/0	0/0	27/6	3/6	5/58
MABLA	7/4	22/6	2/1	0/0	74/7	20/13	9/1	0/0	8/2	6/1	8/1	0/0	0/0	3/1	7/1	20/8	18/51
MPSME	0/0	7/5	4/2	0/0	11/3	20/35	5/1	0/0	4/3	0/0	0/0	0/0	0/0	5/3	7/1	4/5	6/41

TABLE 4. Percent cover of habitat and winter range types in Bear Management Units (BMUs) of the Yellowstone area. Figures separated by a '/' under forest habitat types denote coverages before and after, respectively, the large wildfires of 1988.

Habitat type	Bear Management Unit (BMU)																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Nonforest																		
DRYMD	5	9	9	2	1	4	2	0	4	1	3	5	0	0	1	1	6	1
LITHC	1	1	5	9	2	11	15	0	0	0	1	4	0	0	16	22	7	1
MESMD	10	12	10	8	12	5	4	4	17	5	7	11	1	1	4	2	15	5
TALUS	7	3	4	11	3	14	28	0	1	0	4	3	0	0	2	37	1	4
WETMD	1	2	2	2	1	2	1	2	2	2	2	4	1	4	4	2	5	5
Forest																		
DOPEN	1/1	1/7	1/8	1/15	0/19	2/9	0/3	2/10	1/26	0/23	5/28	3/3	14/30	4/30	1/15	0/0	3/7	4/5
HABLA	4/4	0/0	1/1	0/0	0/0	2/1	4/4	0/0	0/0	0/0	3/3	1/1	0/0	0/0	1/0	7/7	2/1	1/1
HPIAL	26/26	18/17	19/16	30/23	32/18	16/14	15/13	21/19	9/6	4/3	11/9	4/4	6/4	20/13	24/19	17/17	17/17	3/3
HPSME	1/1	2/2	2/2	0/0	0/0	10/10	10/10	0/0	0/0	0/0	0/0	1/1	0/0	0/0	0/0	2/2	0/0	0/0
HVASC	15/15	17/11	21/16	11/4	7/3	9/8	6/4	32/26	34/12	56/40	18/7	10/10	35/23	26/7	28/19	6/6	27/23	21/20
LPICO	2/2	0/0	1/1	0/0	0/0	1/1	0/0	0/0	1/1	14/7	17/8	1/1	6/5	0/0	2/1	0/0	1/1	3/2
MOPEN	1/1	1/5	0/1	1/8	0/18	1/4	1/2	0/3	0/14	0/4	0/15	4/4	3/4	4/12	0/6	0/0	0/1	5/7
LPIEN	5/5	11/9	3/3	6/1	8/5	8/6	11/6	6/6	4/2	1/1	10/1	0/0	0/0	3/2	0/0	1/1	2/2	0/0
MABLA	2/2	11/10	4/3	2/1	5/2	2/1	0/0	21/19	8/6	15/11	5/3	20/20	17/17	6/4	2/1	0/0	7/7	15/15
MPSME	11/11	10/9	15/14	10/7	27/14	8/7	4/6	9/9	19/9	1/1	10/6	26/26	12/12	7/2	7/3	2/2	4/3	28/27
Winter range																		
BIS	0	5	4	5	6	0	0	13	7	15	10	0	0	0	0	0	0	0
EHE	13	20	15	5	12	0	0	1	24	0	17	0	0	1	9	0	4	0
ELE	1	12	9	0	1	23	12	0	13	0	0	0	0	0	0	4	0	0

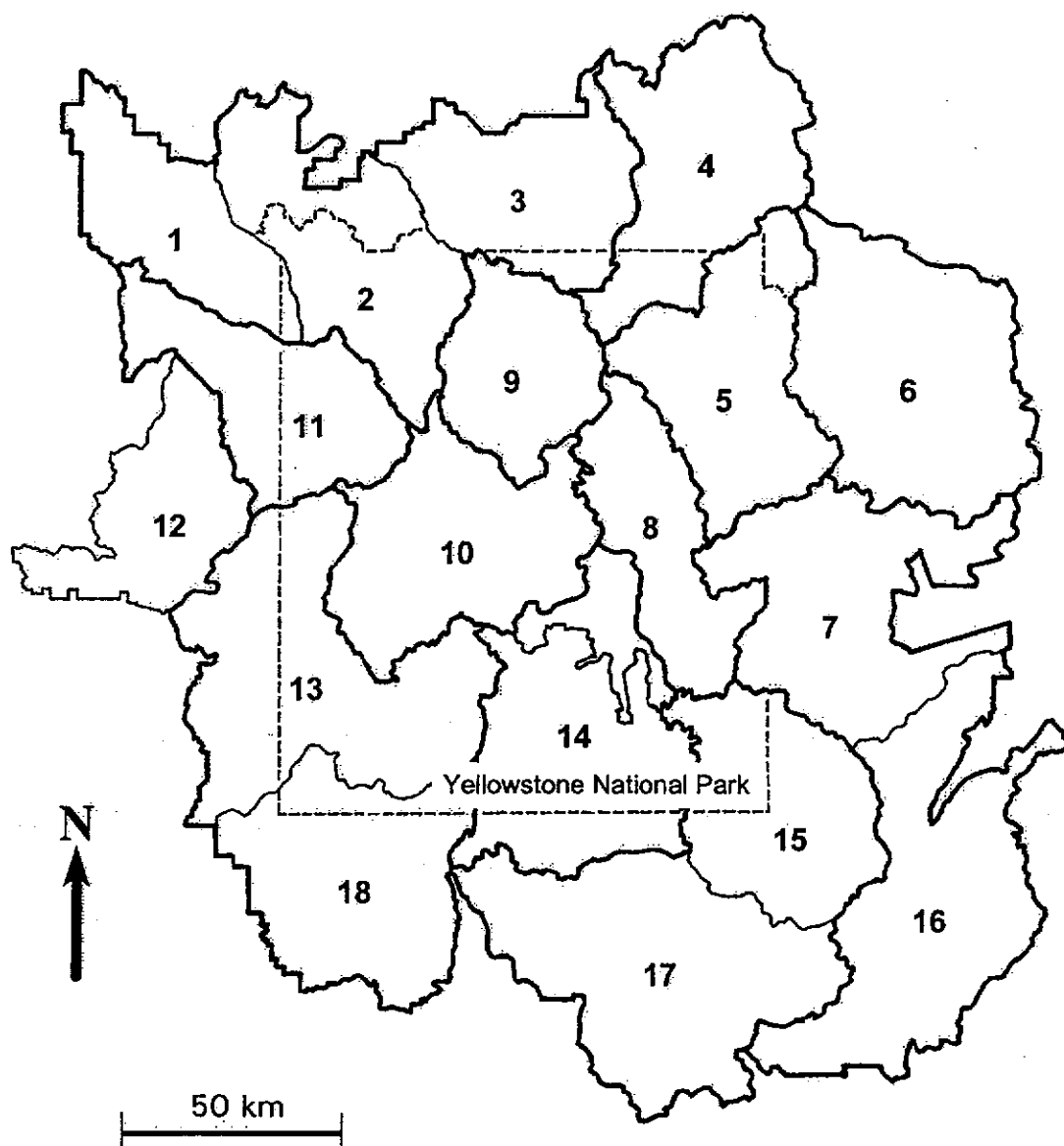


FIG. 6. Map of the Yellowstone study area showing the outer boundary of the Recovery Area, boundaries of individual Bear Management Units (BMUs) within, and, in dashed line, the boundary of Yellowstone National Park. Thicker lines delineate BMUs singly or collectively used to estimate local patterns of activity for female bears. Numbers identify BMUs.

before or after July 31, 1988. Consequently, BMUs were the basis for enumerating habitat types (Table 4). BMUs are about the size of female life ranges ($\sim 900 \text{ km}^2$), and were delineated by management agencies so as to border prominent geographic features (e.g., canyons, mountain crests, and lake shores) and contain spatial aggregations of grizzly bear radiotelemetry locations (Weaver *et al.*, 1986; Fig. 6). BMUs were a logical basis for reckoning the distal effects of general habitat conditions on the relative frequency of different grizzly bear activities within each unit.

I stratified some analyses by three seasons identified as Spring, Estrus, and Hyperphagia (Mattson *et al.*, 1999). Spring started with the emergence of bears from their dens and lasted until 14 May. This coincided with availability of carrion on ungulate winter ranges and peak succulence of graminoids. Estrus lasted from 15 May to 14 July and coincided with mating activity and minimal availability of high quality foods. Hyperphagia lasted from 15 July until bears dened in the fall and coincided with peak feeding activity and potential availability of abundant whitebark pine seeds. I used two seasons (Early and Late) to analyze differences in activities among bear classes, with Early season corresponding to Spring and Estrus and Late season corresponding to Hyperphagia. I treated the three seasons as separate variables in the analysis of movements and home range size introduced. The value of each corresponded to the proportion of radiorelocations from a given bear obtained during that season.

Continuous variables. — Land management agencies in the Yellowstone ecosystem estimated size of the whitebark pine cone crop (number of cones per tree) from permanent transects, 1980–92 (Knight *et al.*, 1993). I estimated crop sizes for 1975–79 (*CONE*) from the proportional volume of pine seeds in grizzly bear feces the following June–July (*WBPV*) using a model that related cone counts to fecal volumes for the period 1980–92 ($CONE = 5.4 + 63.2 \text{ WBPV}^{0.5}$; $r^2 = 0.65$, $MSE = 8.8$, $df = 1 / 9$, $F = 16.6$, $P = 0.003$; Table 5). I calculated volumes of pine seeds in grizzly bear feces, 1977–92, from the results of Interagency Grizzly Bear Study Team fecal analyses (Mattson *et al.*, 1991a). I took volumes for 1975–76 from Knight *et al.* (1977). Estimating crop sizes from fecal volumes is potentially circular with respect to this study's research hypotheses, except that activity at radio locations, not fecal composition, was the analyzed response. I consequently did the analysis relating probability of pine seed use to crop size in two ways: for 1976–92 and only for 1980–92.

TABLE 5. Annual values of distal independent variables used in the analysis of grizzly bear activities and female grizzly bear reproduction in the Yellowstone area, 1977-92. Values in parentheses were estimated from regression models relating number of cones or number of carcasses to volumes of corresponding material in grizzly bear feces.

Year	No. of cones per tree	No. of ungulate carcasses	No. of elk	No. of bison	Indices of winter severity (+4 least severe, -4 most severe)								No. of bears on moth sites
					Northern Range (lower)		Northern Range (upper)		Pelican/ Hayden		Madison/Firehole		
					Bison	Elk	Bison	Elk	Bison	Elk	Bison	Elk	
76	(7.8)		37805	1125	3.0	-2.8	-2.6	-3.2				0	
77	(5.6)	(306)	39047	1252	-2.3	2.4	0.6	1.6				0	
78	(31.2)	(200)	39368	1626	-3.0	0.7	1.9	-0.3		0.7	1.8	0	
79	(9.2)	(57)	40220	1727	-0.1	-0.4	-0.1	-2.0		-0.9	-0.6	0	
80	25.7	(286)	42677	1803	2.8	-2.4	-2.9	-2.0		-1.7	-2.4	1.0	
81	13.2	(14)	41801	2396	-1.1	2.7	1.4	1.7		2.1	0.8	1.0	
82	17.0	(191)	43222	2239	1.7	-1.5	-2.0	-1.2		0.8	0.0	0	
83	17.4	(83)	44022	2160	2.4	-1.6	0.3	-1.3		-0.8	0.2	1.3	
84	6.4	104	46950	2229	0.8	0.7	1.8	-0.2		1.0	2.1	1.5	
85	27.2	51	48230	2456	0.0	0.4	-0.3	0.7		1.8	0.0	2.0	
86	1.4	47	49903	2470	3.1	-1.7	-0.3	-1.5		-2.0	-1.4	3.6	
87	6.1	16	52708	2861	3.5	-1.5	-0.8	-0.5		-0.8	-0.4	4.1	
88	2.4	47	45008	3159	-2.2	0.0	1.0	-0.5		0.8	0.4	4.6	
89	48.8	325	47520	2606	-0.2	-1.6	-1.4	-0.3		-2.3	-2.3	3.9	
90	1.5	6	43274	3178	0.9	-2.8	-1.2	-1.5		-1.8	-0.8	5.6	
91	15.5	(146)	50003	3426	0.5	-1.7	-0.5	-1.9		-2.6	-1.1	7.1	
92	15.4	(29)											

I used numbers of carcasses counted on the Firehole winter range by Green *et al.* (1997), 1984–90, to indicate total number of carcasses on ungulate winter ranges. I used counts from this range in preference to counts from other ranges because grizzly bear scavenging on carcasses during spring was concentrated at higher elevations, in ranges typified by the Firehole area (Green *et al.*, 1997). As with whitebark pine cone crops, I estimated carcass numbers (*CARC*) for other years from a model relating 1984–90 carcass counts to proportional volumes of ungulate remains (*UNGV*) in feces collected during the contemporaneous April ($\ln \text{CARC} = 6.2 + 1.1 \logit \text{UNGV}$; $r^2 = 0.78$, $\text{MSE} = 5.3$, $\text{df} = 1 / 4$, $F = 13.9$, $P = 0.020$; Table 5). I corroborated estimates of carcass availability, 1982–83 and 1991–92, with my field observations and, for remaining years, 1976–1981, by reports in Knight *et al.* (1977, 1978, 1980) and Knight, Blanchard & Kendall (1982).

Because of potential problems with circularity, I also analyzed frequency of carcass use at bear radiotelemetry locations using indices of winter severity as surrogates for carcass counts. I obtained these indices from P. Farnes. Methods for their derivation are described in Farnes, Heydon & Hansen (1999). There is one index for each combination of ungulate species (bison and elk) and winter range type (lower and upper Northern, Pelican/Hayden and Firehole/Madison), excluding elk for Pelican/Hayden. This results in a total of 7 indices for each year back to 1977 with the exception that, prior to 1979, indices were not calculated for the Firehole/Madison winter range (Table 5).

I based annual numbers of elk and bison in the study area on published estimates for the various herds (Mack, Singer & Messaros, 1990; Vales & Peek, 1990; Singer, 1991; Garton *et al.*, 1992; Yellowstone National Park, 1997; Table 5). In some cases, estimates for given herds did not span the full duration of this study. In these instances, I used the first or last estimate as a constant for earlier or later years, respectively. In all cases, these missing data pertained to smaller herds and so this assumption predictably introduced proportionally little error into total numbers estimated for the study area. I assumed that the proportional distribution of elk and bison (by BMU) correlated with the extent of corresponding winter ranges. I therefore represented the local abundance of ungulates by the combined effects of winter range proportions and annual population estimates.

I used monthly basin-wide summaries of precipitation (ppt) and temperature for the Yellowstone and Snake River drainages, taken from the U.S. Department of Commerce State

Climatic Summary for Wyoming, to represent ecosystem-wide climate and weather, 1976–1992. I defined winter ppt as the total for November–March. I defined cumulative growing season ppt as the total for April through the month of interest. I used ppt and temperature, transformed to cm and °C, to represent monthly weather, assuming that absolute amounts of ppt and deviations of mean temperatures above freezing are biologically and physically meaningful.

Statistical models

Home range size and movements. — Conceptually, some relations between range sizes or movements and bear- or habitat-related factors were causal while others were correlational. I theorized that sample size, season, class-of-bear, size-of-bear (*LBM*), and occurrence of a management translocation (treated as a dummy variable; 0 = no, 1 = yes) potentially contributed to explaining range size and movements. Conversely, activities of bears were logically treated as correlates of movements or range sizes; i.e., the extent of movements could both affect and be affected by the activities undertaken by bears. Even so, I used multiple regression because of my interest in an integrated analysis of all relations, but with careful interpretation of relations between dependent and independent variables, especially those related to frequencies of activities.

Individual bears constituted units of analysis. I weighted the contribution of each bear by the sample size used to estimate proportions of activities. Estimates based on greater numbers of observations thus contributed more to the results of this analysis. I natural-log transformed range sizes and movement distances to normalize distributions. I natural-log transformed percentages of bear locations by season and bear class and percentage of bear activity by type to linearize relations (Weisburg, 1985; Johnson & Wichern, 1992).

Corpulence and body size. — Again, many of the relations between body dimensions and movements or types of activity were more defensibly treated as correlations. Body dimensions could both affect and be affected by activities or the magnitude of movements undertaken by a bear. However, for the same reasons expressed for the analysis of movements and home range sizes, I used multiple regression analysis subject to cautious interpretation. As above, I used individual bears weighted by sample size as units of analysis.

The analysis of relations between activities and body dimensions was complicated by the fact that measurements of body dimensions were often collected before or midway through the period during which data were collected to estimate proportional activity. If regression analysis was to disclose information regarding the effects of feeding activity on corpulence or body size, then only body dimensions obtained mid-way through or at the end of the data collection period logically would be included in the analysis. Consequently, I analyzed the data two ways: (1) using all measures of body dimensions ('initial' and 'terminal' measures) and (2) only using dimensional measures obtained mid-way through or at the end of the sampling period for each bear ('terminal' measures). Results of the latter analysis should better reflect the effects of diet on morphology whereas the inclusive analysis (all measures) should better reflect the effects of body size or condition on subsequent activity.

Reproduction. — As with range size and movements, I theorized that there were a mix of 'causal' or correlative relations between total production or loss of cubs by females and factors related to time, age, morphology, and activity. I assumed that the effects of female age and duration (in yrs) of observation were causal in nature. On the other hand, I theorized that reproduction both affected and was affected by lean body mass, corpulence, and types of activity. However, as with the two previous analyses, I used multiple regression, subject to cautious interpretation, as a framework for integrating the analysis. I used individual bears as units of analysis weighted by number of observations of activity for each. I reckoned age as the median for the period of observation for each female. I treated age as a polynomial because I speculated effects related to maturation and senescence. Because year, as a covariate, might not adequately control for the effect of passage of time on number cubs observed or subsequently lost, I analyzed these relations according to length of years of observations in two sets: ≥ 1 yrs and ≥ 3 yrs.

I also analyzed cub production and loss reckoned as the likelihood per female per year, treating females by year as units of analysis. I used logistic regression analysis to estimate the effects of generalized feeding activity by females in a given BMU and study-area-wide annual levels of whitebark cone production, army cutworm moth use, and ungulate carcass availability. I also included female age in these models, again expressed as polynomials representing the potential effects of maturation and senescence. I estimated the

generalized female diet, by BMU, from models described for each activity in the Results, controlling for the effects of annual variability in weather and abundance of key foods (Table 6). I transformed independent variables in various ways to insure a logistic form to the response and used R^2_L to help judge adequacy of model fit to the data (Demaris, 1992).

These two approaches were favored by different considerations. The first approach explicitly related observed diet of an individual female to observed cub production and loss. However, there is evidence that female bears buffer themselves, or 'average-out', temporal and spatial variation in food abundance by their behavior and ample adipose reserves (Stirling & Derocher, 1990; Pond *et al.*, 1992; Ramsay, Mattacks & Pond, 1992; Atkinson *et al.*, 1996). Contemporaneous estimates of diet may not relate well to observed reproduction because of considerable lags in dietary effects. The second approach thus has the advantage of generalizing dietary effects in a way that perhaps mimics the somatic and behavioral buffering available to most female bears. As mentioned before, the second approach also takes advantage of all data on reproduction of captured females, rather than being limited to a subset of females that were prone to survive and be recaptured.

Likelihood and levels of different activities. — I also used logistic regression analysis to estimate the effects of independent variables on the likelihood that a bear had engaged in a specific activity at a given radiotelemetry location. Radiotelemetry locations were units of analysis and bear class and Julian date were among a number of putative effects. I modeled each of 20 activities separately, with the probability of the activity of interest = 1 and the probability of all other activities = 0. The proportional frequency of activities did not sum to 1 across all radiotelemetry locations because more than one activity was documented at many locations. I theorized different subsets of candidate effects for each type of activity based on prior knowledge so as to avoid 'data dredging' and the attendant risk of over-fitted models (Burnham & Anderson, 1998). I analyzed several activities by season because the target food changed substantially in terms of nutrient composition or vulnerability despite being taxonomically the same. This held for ungulates, which I analyzed by all three seasons, and for graminoids and rodents, which I analyzed by Early and Late seasons (see above).

Given that a specific type of activity had occurred, I used multiple linear regression to estimate the effects of independent variables on the level of that activity. In this way, I analyzed the effects of various factors on grizzly bear activities at two hierarchical levels: (1)

TABLE 6. Estimated relative percent frequency of feeding activities by female grizzly bears, 1977–92, in different regions of the Yellowstone area defined on the basis of Bear Management Units (BMUs). Annual variability in weather and abundance of key foods was controlled through the use of models that incorporated such effects. Feeding activities are described in Table 1.

BMU	Feeding activity							
	WBP	PRT	FAT	ROO	HGM	INS	LGM	LRD
1, 2 & 3	4.5	0.7	0.5	9.8	12.8	9.7	0.8	0.3
5	9.7	1.8	0.4	7.9	11.2	14	0.5	0.1
6	1.5	<0.1	1.5	6.7	7.9	16.3	0.5	0.1
7 & 16	10.7	0.9	1.8	5.0	7.9	12.1	0.5	<0.1
8	4.0	1.2	<0.1	8.1	8.4	11.4	1.2	0.2
9	3.6	1.3	0.1	14.9	12.0	4.5	0.6	0.1
10	1.8	5.9	0.8	3.8	9.2	9.0	0.7	0.1
11	2.6	1.0	<0.1	0.5	5.2	32.7	0.2	0.1
13, 15, 17 & 18	4.7	0.9	<0.1	7.5	8.6	10.1	0.4	0.1

the likelihood that an activity would occur and (2), given that it had occurred, its level. This approximated a hierarchy of choice by bears regarding whether they would engage in an activity and, if so, how intensively for how long. I reckoned 'levels' in terms of field measures, described above, that were unique to each type of activity. In instances where numbers of feces were used, responses were more definably discrete. Use of logistic in preference to least squares regression is recommended if counts of responses were ≤ 4 (Demaris, 1992). Such was the case for grazing of graminoids by grizzly bears during Spring and Estrus. For this activity, I used logistic regression to model the likelihood of ≥ 1 (0 = not present, 1 = present) and ≥ 2 feces at a site.

Finally, I used logistic regression analysis to specify models describing differences in habitats used by different classes of bear. I constructed two models (Early and Late season) for each pairwise comparison of habitat use by adult males or females with COY with all other classes of bear. I used R^2_L to judge the relative degree of overlap in habitat use between the two classes of bear in each comparison. A value of R^2_L approaching 1 signified virtually no similarity (complete discrimination) while a value of R^2_L approaching 0 signified virtually no differentiation. All conclusions regarding overlap or similarity were conditional on the candidate effects in each model. I construed 'habitat use' in terms of distal and proximal landscape or site features rather than spatial and temporal coordinates (*cf.* Mace & Waller, 1997).

Results

Field crews documented activity and site features at 1866 telemetry locations of radiomarked grizzly bears in the Yellowstone area, 1977–92. Of these, 1181 were locations of female bears and 685 were locations of male bears, with 309 from subadult males, 376 from adult males, 205 from subadult females, 262 from adult females unaccompanied by dependent young, 265 from females accompanied by cubs-of-the-year (COY), 251 from females accompanied by yearlings, and 171 from females accompanied by older young. Some locations were not attributed to an age class or reproductive status. A total of 46 females and 35 males had sufficient numbers of observations to be used in the analysis individual bear histories. Sample sizes in most statistical analyses varied because data were missing for some variable.

Activities

Use of whitebark pine seeds

Use of pine seeds was more frequent following and especially during years when more cones were produced (Table 7). This held, even accounting for effects of proximal site features including the abundance of whitebark pine. The extent of excavations for pine cones in red squirrel middens was sensitive to size of the contemporaneous cone crop whereas the number of cones excavated was more sensitive to size of the previous year's crop (Table 8; Fig. 7d). At the distal scale, likelihood of whitebark pine seed use was greater in Bear Management Units (BMUs) where there was proportionally more whitebark pine forest and talus or alpine vegetation (Fig. 8a). Depending on the model, use of pine seeds was less likely during years when bison or elk were most numerous and ungulate carcasses had been abundant during Spring. Proximal features — whitebark pine basal area, total overstory basal area, and amount of coarse woody debris — 'screened out' effects of the regional extent of whitebark pine forests and rock and alpine habitats as well as the effects of ungulates. The relative frequency of pine seed use peaked at intermediate levels of woody debris and whitebark pine basal area (Figs. 7a & 7c).

Time and type of bear also affected the probability that whitebark pine seeds were used. Females were nearly twice as likely as males to consume whitebark pine seeds, especially during Hyperphagia (Table 7; Fig. 8c). Subadults also were slightly more prone than adults to use pine seeds. Both the likelihood of use and the extent of related excavations

TABLE 7. Logistic regression models for the logit-transformed probability that a bear had been feeding on whitebark pine seeds, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, vegetation features, type of bear, and time for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	All years (distal factors only)			1980–1992 (distal factors only)			All years (wt. proximal factors)		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-3.4	1.1		56	16		-8.9	0.92	
Food availability in the ecosystem									
# of whitebark pine cones (n/tree)	0.50†	0.15	9.6	0.92†	0.17	35.0	0.74†	0.22	9.6
# of whitebark pine cones, previous yr (n/tree)							0.021	0.013	0.7
# of ungulate carcasses	-0.52†	0.12	68.3						
# of bison				-10†	2.3	20.9			
# of elk	$-2.7 \times 10^{-9}†$	6.6×10^{-10}	16.9						
Extent of habitat types (% of BMU)									
Whitebark pine forest	0.0014†	0.00032	15.2	0.0011†	0.00041	6.8			
Alpine & talus	0.0015†	0.00031	18.5	0.042	0.0096	18.2			
Vegetation features									
Whitebark pine basal area (m ² /ha)							2.8†	0.34	125.2‡
Whitebark pine basal area ²							-0.60†	0.10	
Total forest basal area (m ² /ha)							0.032	0.0069	18.3
Amount of woody debris (index)							0.70	0.24	22.8‡
Amount of woody debris ²							-0.065	0.032	
Type of bear									
Gender (female)	0.39	0.11	11.7	0.50	0.14	15.3			
Age (adult)				-0.29	0.12				
Time									
Julian date	0.000059†	4.9×10^{-6}	173.7	0.024	0.0026	132.0	0.000027†	6.7×10^{-6}	23.0
Sequential year	1.2§	0.36	12.2	3.8§	0.83	25.2			
Post-1988 fires	-0.81	0.23	13.2	-0.41	0.19	4.7	-0.70	0.19	12.6
Statistics									
χ^2 (df)	718	(1512)		579	(1276)		421	(1353)	
P	1.000			1.000			1.000		
R_L^2	0.69			0.70			0.80		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§Coefficient was estimated for the square root of the independent variable.

|This Δ value includes the effects of removing both terms of the polynomial for this variable.

TABLE 8. Multiple regression models of the relations of extent of excavations or number of cones per dm³ of excavation for whitebark pine cones at a site where feeding of this type occurred, to food abundance, temperatures, and time, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Whitebark pine (dm ³ of excavations)†			Whitebark pine (# of cones/dm ³ of excavation)†		
	β_i	SE	Δ	β_i	SE	Δ
Constant	0.47	0.78		0.97	0.15	
Food abundance						
# of whitebark pine cones (<i>n</i> /tree)	0.00085‡	0.00016	9.0			
# of whitebark pine cones (<i>n</i> /tree), previous yr				0.029	0.011	0.5
Current month's temp. (°C)	0.0061‡	0.0022	1.0			
Time						
Julian date	0.000033‡	0.0000093	3.0			
Post-1988 fires	-1.2	0.31	3.5			
Statistics						
<i>F</i> (num. df / den. df)	11.8	(4 / 68)		6.9	(1 / 30)	
<i>P</i>	0.000			0.013		
<i>R</i> ²	0.41			0.19		

†Coefficient was estimated for values of the dependent variable (*y*) transformed as $\ln ([y] + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

Whitebark pine

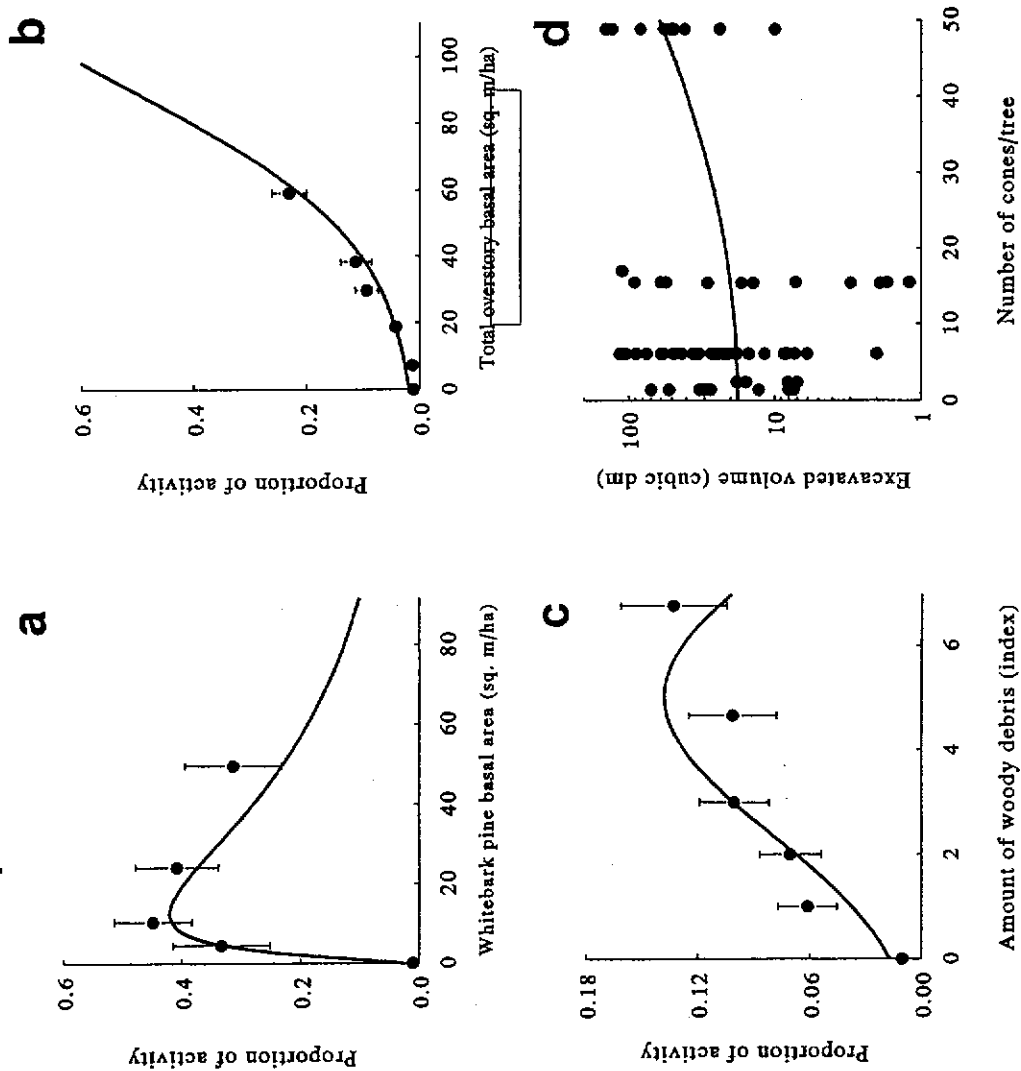


FIG. 7. Relations between grizzly bear use of whitebark pine seeds in the Yellowstone ecosystem, 1977-92, and variables denoting vegetation structure or abundance of seeds. Bear use is signified either as the proportion of total activity involving use of pine seeds or the volume excavated by a bear to obtain seeds from a red squirrel midden. Points bracketed by standard error bars are proportions for quintiles or octiles shown to illustrate goodness-of-fit.

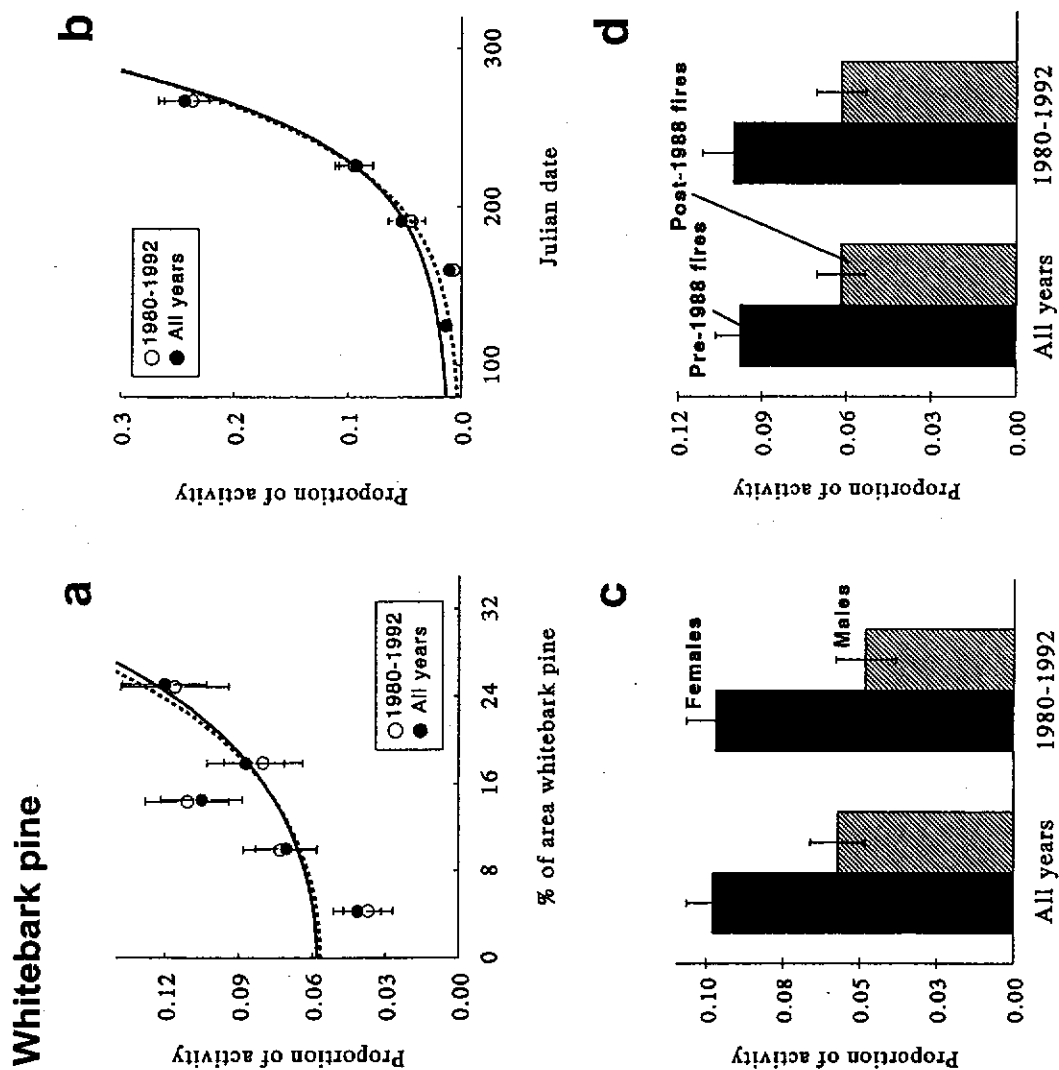


FIG. 8. Relations between grizzly bear use of whitebark pine seeds in the Yellowstone ecosystem, 1977-92, and variables denoting distal effects of landscape features, food abundance, date, gender, and the fires of 1988. Bear use is signified as the proportion of total activity involving use of pine seeds. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

increased substantially with time-of-year (Fig. 8b). Likelihood of use also tended to increase during the study, with the caveat that likelihood of use and extent of excavations declined substantially after the fires of 1988 (Fig. 8d). Controlling for all other effects, likelihood and intensity of use declined by 45–50% (depending on the model) and 30%, respectively. Thus, a trend towards increasing use was contravened by the effects of extensive wildfires.

Use of ungulates

During Spring, the likelihood of scavenging by grizzly bears was positively related to number of ungulate carcasses on winter ranges and cumulative growing season precipitation (ppt), and negatively related to the extent of whitebark pine forests in the surrounding BMU (Table 9; Fig. 9b). None of the winter severity indices substituted for counts of ungulate carcasses. Proximal site features screened out the effects of weather and habitat types. Likelihood of scavenging decreased with the amount of live forest basal area, the extent of total vegetation ground cover, distance from a forest/non-forest edge, and increases in elevation (Table 10).

During Estrus there was again a greater likelihood that bears would prey on or scavenge an ungulate when there was greater winter-kill and greater cumulative growing season ppt (Table 9; Fig. 9c). Females with COY also tended to use ungulates less often during Estrus compared to other bears. The effect of class of bear was screened out by the local positive effects of live forest basal area, forb ground cover, and distance to forest edge (Table 10; Figs. 9a & 10b). Considering proximal effects, grizzly bears also were more likely to consume ungulates during Estrus in areas with more extensive bison winter range.

During Hyperphagia, grizzly bear consumption of ungulates was positively related to the extent of whortleberry-type forests in the surrounding area and negatively related to cumulative growing season ppt (Tables 9 & 10; Fig. 9d). Likelihood of use also was higher for adults and for males compared to females or subadults (Fig. 9a). Considering proximal effects, likelihood of ungulate use during Hyperphagia also was greater during years of larger whitebark pine seed crops and during drier months. Proximal features, including forb and graminoid ground cover and distance to forest/non-forest edge, screened out the effects of cumulative growing season ppt and class-of-bear (Table 10; Fig. 10b). Grizzly bears were more likely to use ungulates farther from forest/non-forest edges and where there was more extensive forb and graminoid ground cover.

TABLE 9. Logistic regression models for the logit-transformed probability that a bear had been feeding on an ungulate carcass, related to variables pertaining to distal effects including carcass numbers, extent of habitat types, weather, and type of bear, for grizzly bears in the Yellowstone ecosystem, 1977-92. Models are presented for each of the 3 seasons. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Spring			Estrus			Hyperphagia		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-1.6	0.84		-5.9	1.1		-2.4	0.76	
# of ungulate carcasses	0.000017†	4.7×10^{-6}	11.8	0.35†	0.19	1.8			
Extent of habitat types (% of BMU)									
Whitebark pine forest	-0.59	0.33	2.1						
Whortleberry-type forest							0.00059†	0.00017	8.9
Cumulative growing season ppt. (cm)	0.0013†	0.00065	15.4	0.012†	0.0035	9.1	-0.82†	0.38	2.4
Type of bear									
Reproductive status (wt. COY)				-0.44	0.25	5.7			
Gender (female)							-0.43	0.19	3.0
Age (adult)							0.49	0.24	2.8
Statistics									
χ^2 (df)	86.5	(101)		35.2	(55)		185.3	(377)	
P	0.848			0.983			1.000		
R_c^2	0.53			0.80			0.79		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

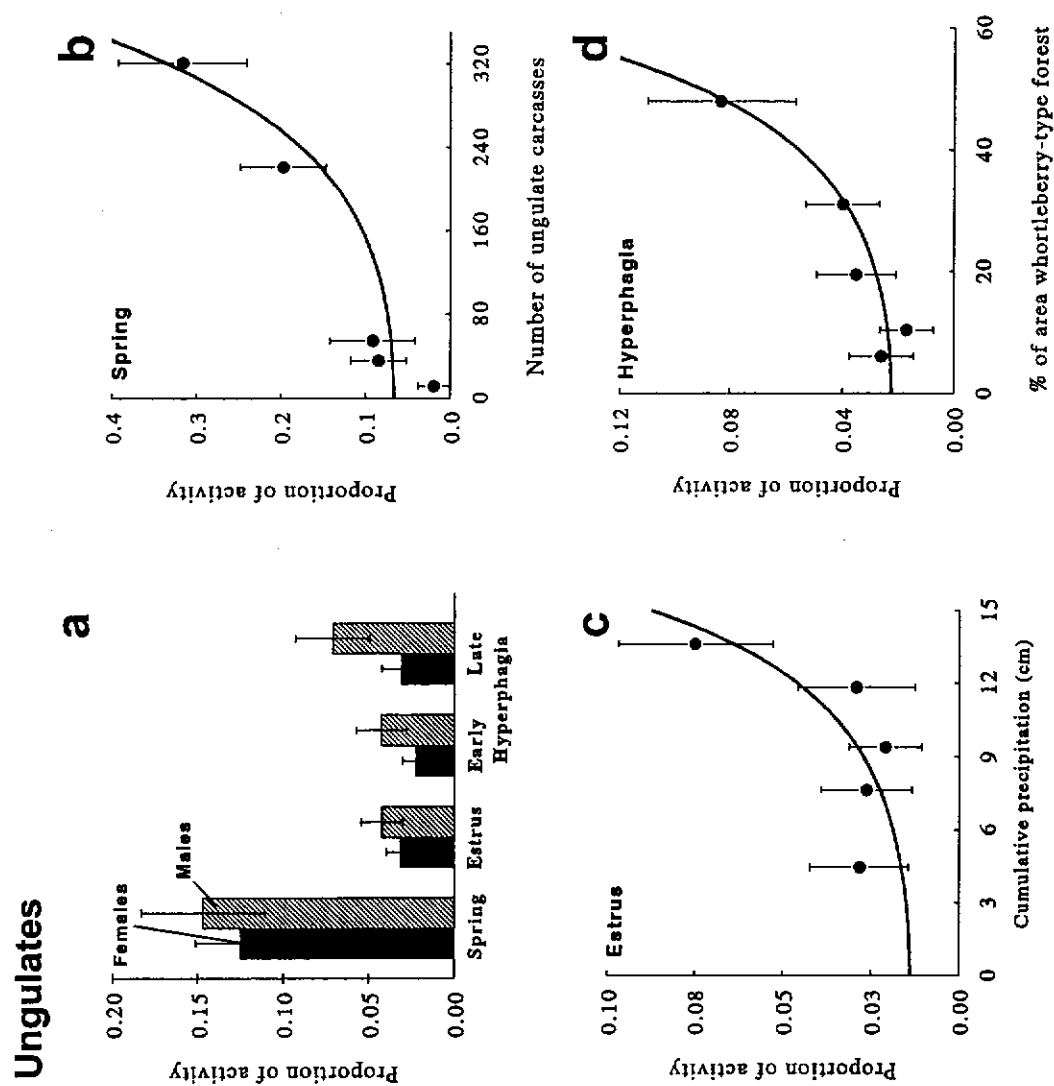


FIG. 9. Relations between grizzly bear use of ungulates in the Yellowstone ecosystem, 1977-92, and variables denoting effects of season, gender, ungulate carcass availability, weather, and extent of whortleberry-type forests. Bear use is signified as the proportion of total activity involving use of ungulates. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 10. Logistic regression models for the logit-transformed probability that a bear had been feeding on an ungulate carcass, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, vegetation and site features, and weather, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Spring			Estrus			Hyperphagia		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	81	27		-8.8	1.5		-4.7	0.94	
Food availability in ecosystem									
# of ungulate carcasses	0.000018†	5.6×10^{-6}	9.0	0.58†	0.21	6.6			
# of whitebark pine cones (n/tree)							0.49†	0.26	1.7
Extent of habitat types (% of BMU)									
Bison winter range				0.53†	0.25	3.4			
Whortleberry-type forest							0.033	0.013	3.9
Vegetation features									
Live forest basal area (m ² /ha)	-0.31†	0.18	1.0	0.00037†	0.00016	2.0			
Total vegetation ground cover (%)	-0.42†	0.20	2.4						
Forb ground cover (%)				0.00081†	0.00026	6.6	0.00052†	0.00023	2.4
Graminoid ground cover (%)							0.00063†	0.00015	16.1
Distance to forest edge (m)	-0.40†	0.13	8.0	0.00066	0.00034	0.7	0.21†	0.13	9.7
Elevation (m)	-10†	3.6	7.3						
Weather									
Cumulative growing season ppt. (cm)				0.012†	0.0041	7.0			
Current month's ppt. (cm)							-1.7†	0.52	10.1
Statistics									
χ^2 (df)	114	(176)		159	(562)		168	618	
P	1.000			1.000			1.000		
R_c^2	0.55			0.80			0.81		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x+1)$.

‡Coefficient was estimated for squared values of the independent variable.

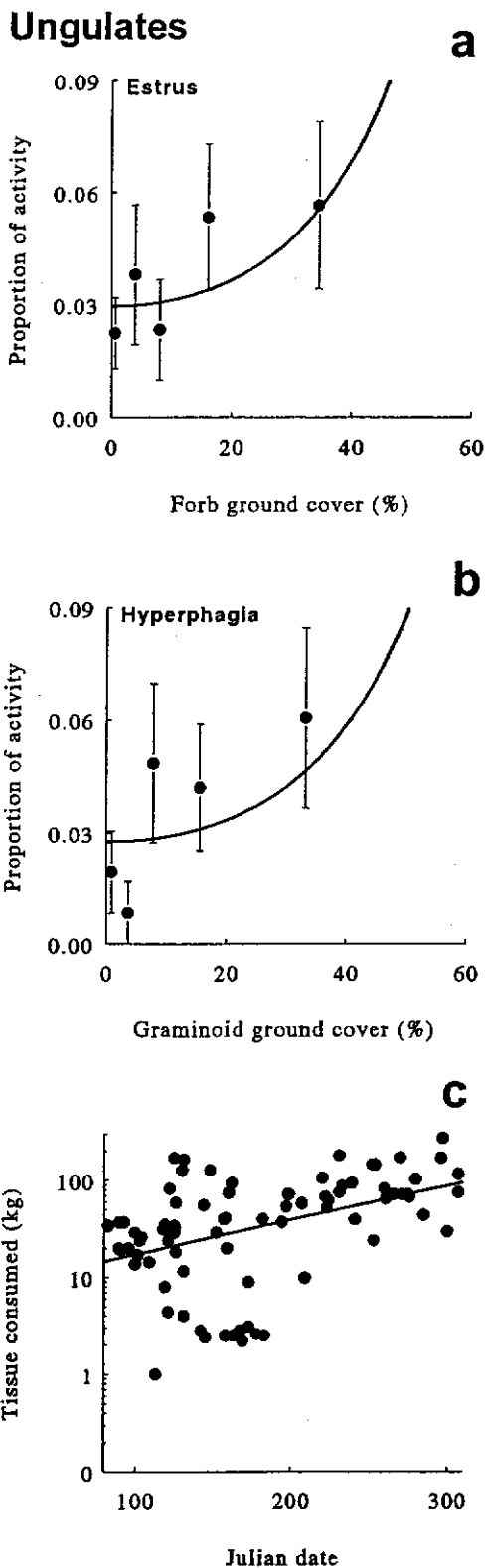


FIG. 10. Relations between grizzly bear use of ungulates in the Yellowstone ecosystem, 1977-92, and variables denoting effects of forb or graminoid cover and date. Bear use is signified either as the proportion of total activity involving use of ungulates or the total tissue consumed by bears from a carcass. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

Aside from the expected effects of species and age-class of ungulate (Table 11), the amount of tissue estimated to have been consumed by grizzly bears from an ungulate carcass was related to date, sequential year, and forest and site features (Table 11). All else equal, more tissue was consumed later in the season (Fig. 10) and in forests with greater forest basal area, but little lodgepole pine or shrub ground cover. Interestingly, more tissue was consumed from a given carcass by subadult versus adult bears and earlier versus later in the study period.

Use of roots

Yampa roots were more likely used in areas with extensive mesic and wet non-forest habitats, during wet months, and by subadult and female bears (Table 12; Figs. 11a & 13c). Use peaked during the warmest months and later in the growing season (Table 12; Fig. 12c). The positive effects of yampa abundance (Fig. 13a), advanced yampa phenology, and graminoid and shrub abundance (Fig. 14d), together with the negative effects of elevation and total forest basal area, screened out the effects of date, age-of-bear, and extent of non-forest habitats (Table 13). Yampa abundance had a predictably positive effect on the total number of excavations for this root at a feeding site (Table 14; Fig. 13b). Number of excavations also was positively related to cumulative growing season ppt and date. The number of yampa roots obtained per individual excavation was positively related to date, graminoid cover, and intermediate amounts of dead standing basal area, but negatively related to shrub cover (Table 14). Number of roots per excavation increased with increasing cumulative growing season ppt and when a subadult bear was involved.

Biscuitroots more often were used by bears in areas with extensive mesic non-forest habitats, whitebark pine forests, or low-elevation elk winter range as well as following years when large whitebark pine cone crops were produced (Table 12). Use also was more likely during warm wet months following dry winters, but earlier in the growing season compared to yampa (Table 12; Figs. 12a & 12b). Also in contrast to yampa, adults more often excavated biscuitroots compared to subadults (Fig. 11b). Biscuitroot abundance and phenology together with other proximal sites features screened out most distal effects, including those of temperature, cone crop size, date, and extent of habitat types (Table 13). Biscuitroot was more likely dug at higher elevations where biscuitroot was abundant and phenologically advanced and where mature trees were sparse and total vegetation ground

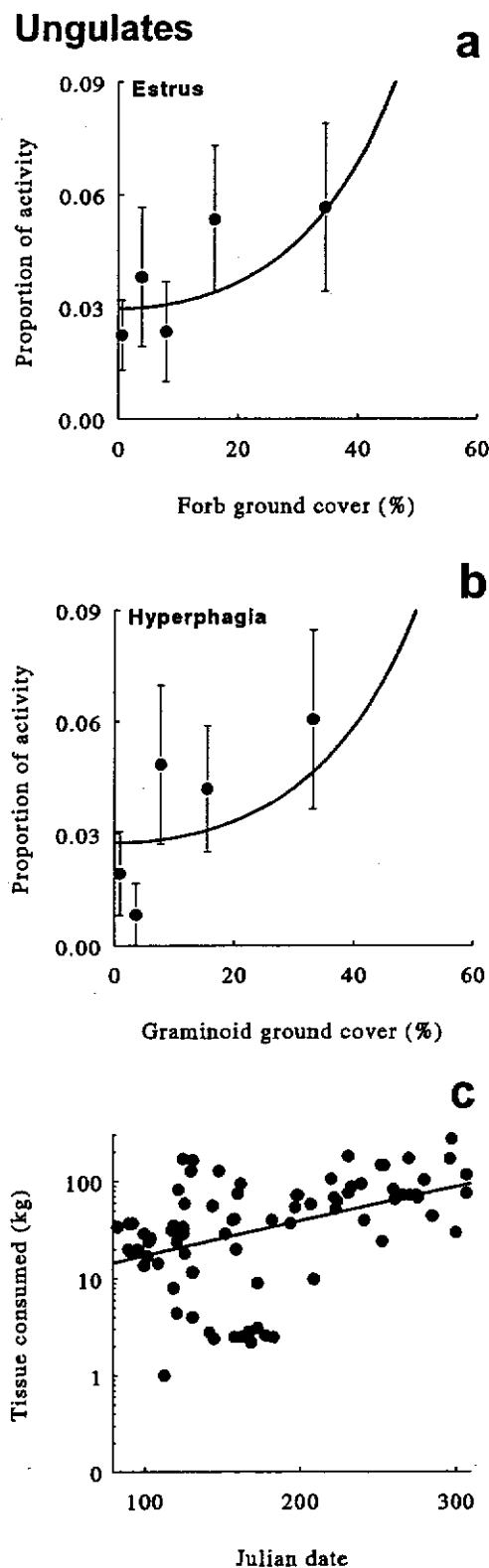


FIG. 10. Relations between grizzly bear use of ungulates in the Yellowstone ecosystem, 1977-92, and variables denoting effects of forb or graminoid cover and date. Bear use is signified either as the proportion of total activity involving use of ungulates or the total tissue consumed by bears from a carcass. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 12. Logistic regression models for the logit-transformed probability that a bear had been feeding on roots of yampa, biscuitroot, or osmorhiza, related to variables pertaining to distal effects including food availability, extent of habitat types, weather, type of bear, and date for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Yampa			Biscuitroots			Osmorhiza		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-21	4.0		-10	3.0		-4.8	0.96	
Food availability									
# of whitebark pine cones (n/tree)							-1.0†	0.26	19.9
# of whitebark pine cones, previous yr (n/tree)				0.00065‡	0.00015	14.6			
# of bison				8.7×10^{-4} ‡	4.8×10^{-4}	1.4			
Extent of habitat types (% of BMU)									
Mesic non-forest	0.0044‡	0.0011	13.6	0.068	0.025	5.6			
Wet non-forest	0.27	0.14	1.5						
Whitebark pine forest				0.0016‡	0.00054	6.9			
Low-elevation lodgepole pine forest							-1.4†	0.49	10.9
Mesic subalpine fir forest							0.14	0.040	15.2
Low-elevation elk winter range				0.47†	0.12	13.5			
High-elevation elk winter range							0.058	0.025	4.8
Weather									
Current month's ppt. (cm)	0.16	0.059	4.8						
Cumulative growing season ppt. (cm)				2.4†	0.50	29.5			
Total winter ppt. (cm)				-1.8†	0.47	14.5			
Current month's temperature (°C)	0.0075‡	0.0017	20.0	2.4†	0.51	26.8			
Type of bear									
Gender (female)	0.48	0.16	8.3						
Age (adult)	-0.27	0.14	1.9	0.69	0.19	16.1			
Julian date	2.7†	0.72	13.9	-0.00002‡	0.000012	2.1	0.000028‡	6.3×10^{-6}	19.4
Statistics									
χ^2 (df)	486	(1605)		456	(1500)		195	(1375)	
P	1.000			1.000			1.000		
R_L^2	0.79			0.80			0.91		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

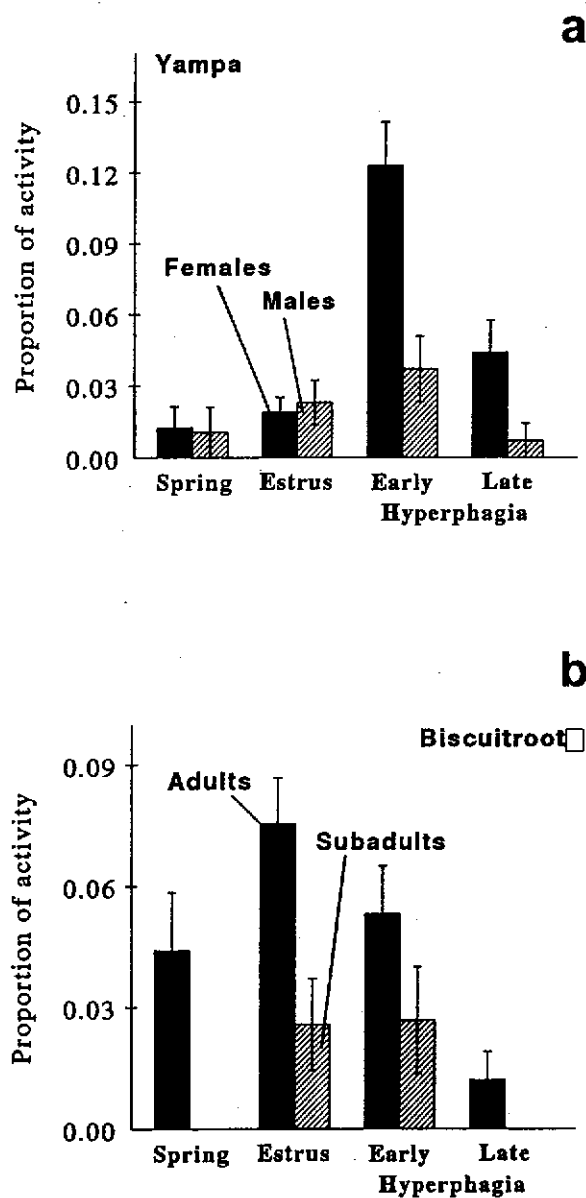


FIG. 11. Relations between grizzly bear use of yampa and biscuitroot roots in the Yellowstone ecosystem, 1977-92, and variables denoting effects of season and class-of-bear. Bear use is signified as the proportion of total activity involving use of the indicated species.

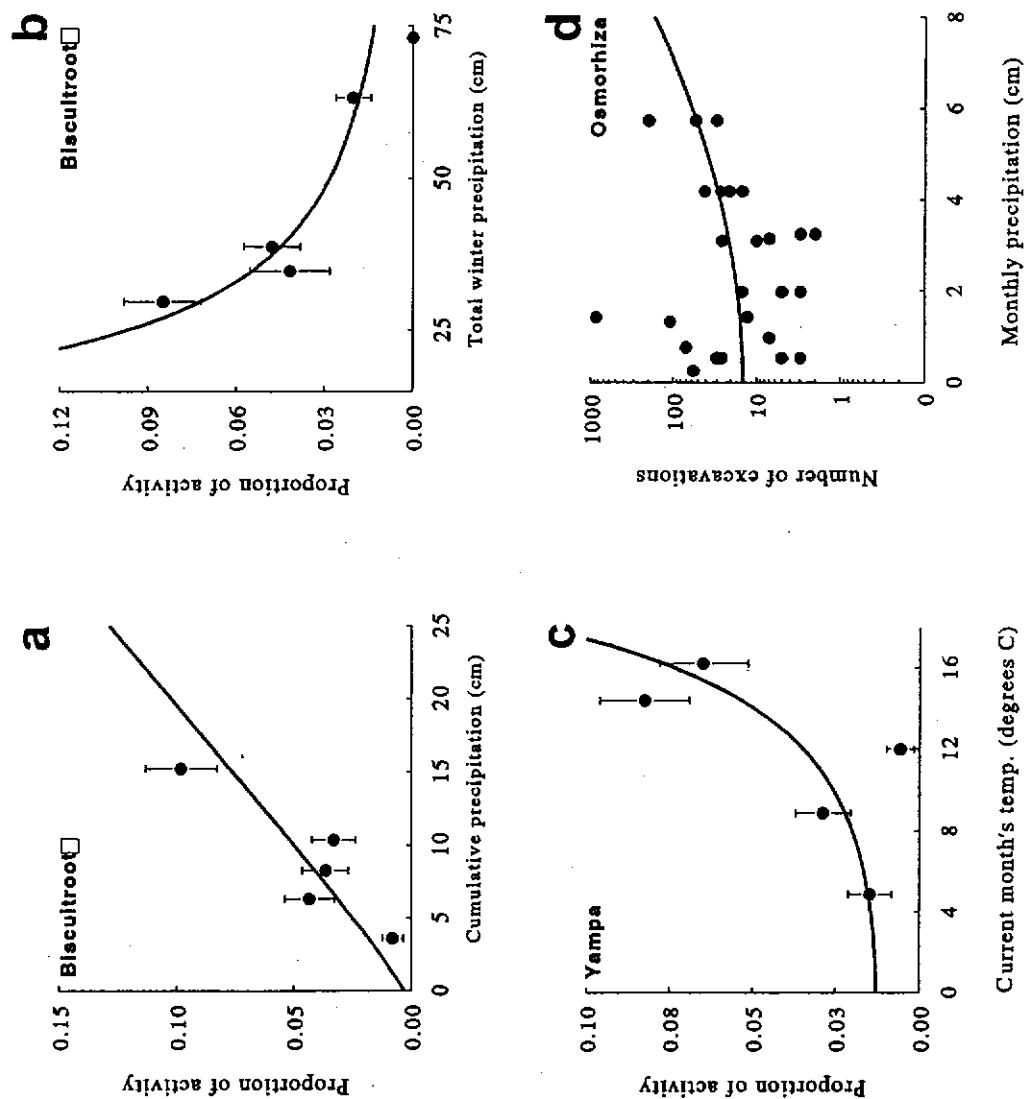


FIG. 12. Relations between grizzly bear use of various roots in the Yellowstone ecosystem, 1977-92, and variables denoting effects of weather. Bear use is signified either as the proportion of total activity involving use of indicated species or as the total number of excavations at a feeding site. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

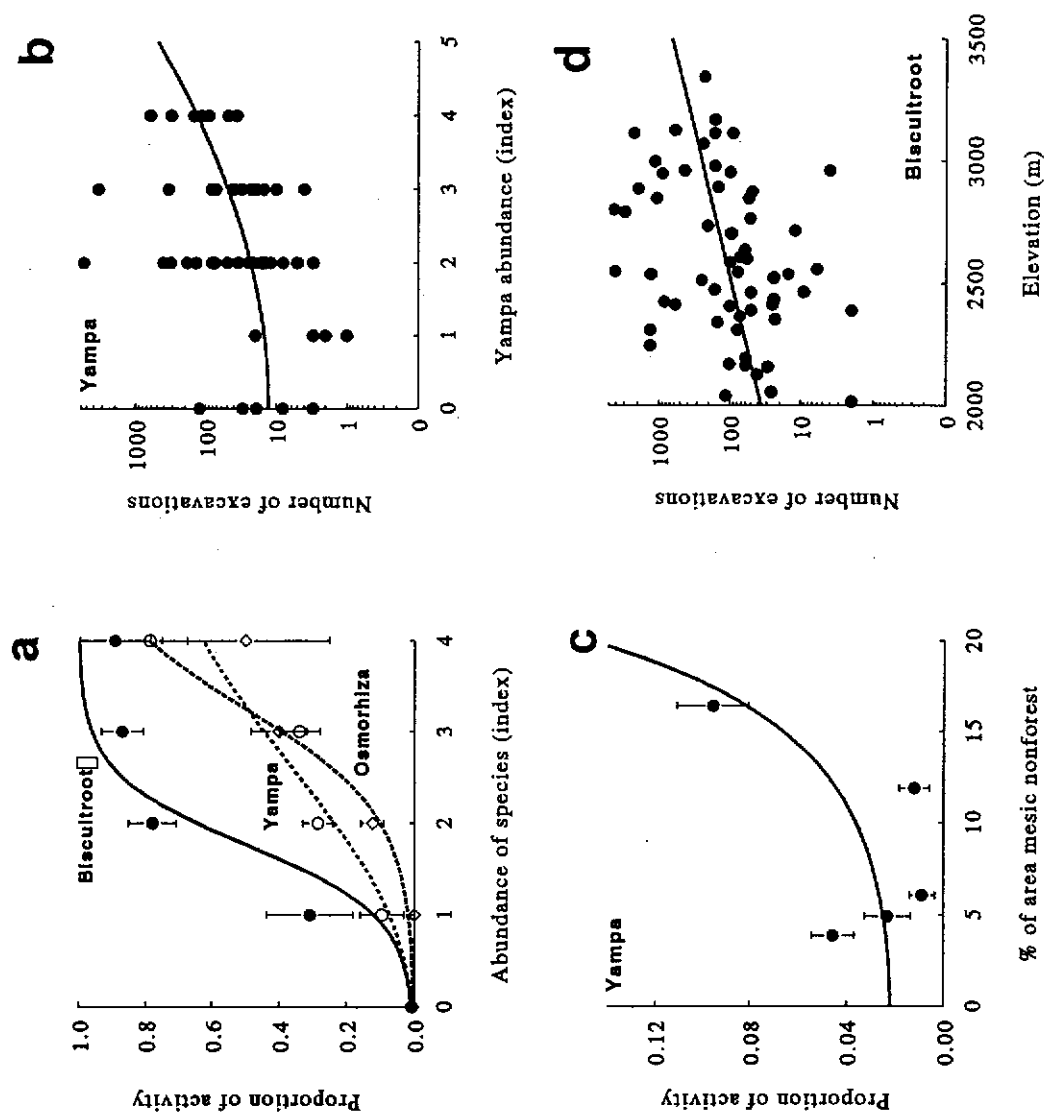


FIG. 13. Relations between grizzly bear use of various roots in the Yellowstone ecosystem, 1977-92, and variables denoting effects of species abundance and elevation at a feeding site as well as extent of mesic non-forest sites in the surrounding BMU. Bear use is signified either as the proportion of total activity involving use of roots or as total number of excavations at a feeding site. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

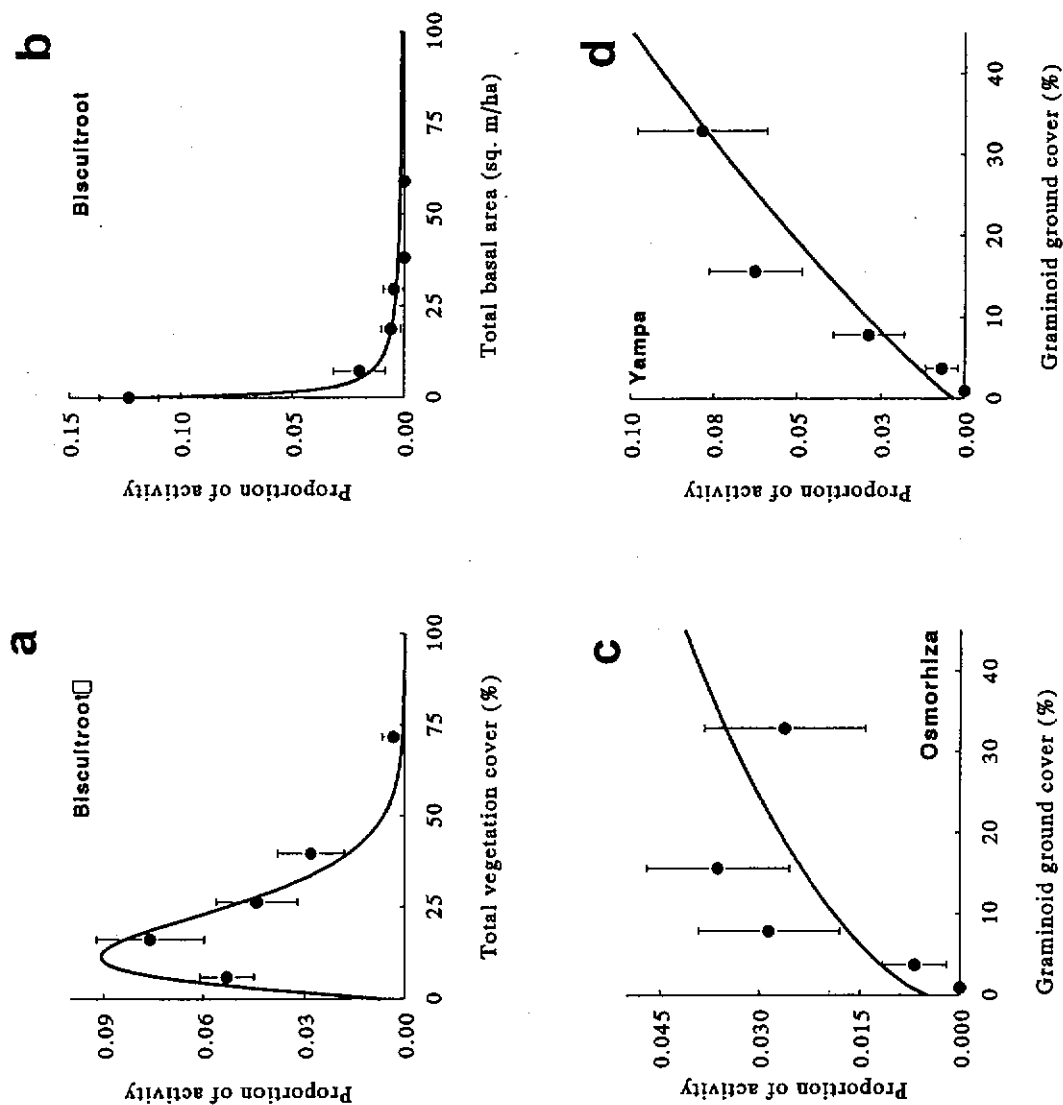


FIG. 14. Relations between grizzly bear use of various roots in the Yellowstone ecosystem, 1977-92, and variables denoting effects of vegetation structure and cover at a feeding site. Bear use is signified as the proportion of total activity involving use of roots. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 13. Logistic regression models for the logit-transformed probability that a bear had been feeding on roots of yampa, biscuitroot, or osmorhiza, related to variables pertaining to distal and proximal effects including extent of habitat types, food abundance, vegetation features, elevation, weather, gender, and time for grizzly bears in the Yellowstone ecosystem 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Yampa			Biscuitroots			Osmorhiza		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-6.8	1.9		-2.8	5.5		-16	2.7	
Extent of habitat types (% of BMU)									
Low-elevation elk winter range	0.35†	0.16	2.8						
Whortleberry-type forest							0.0019‡	0.00083	3.9
Low-elevation lodgepole pine forest							-0.36	0.13	7.2
Food abundance									
Yampa abundance (index)	3.2†	0.44	70.9						
Biscuitroot abundance (index)				0.25†	0.098	5.9			
Osmorhiza abundance (index)							1.8	0.37	32.9
Yampa phenology (index)	0.042†	0.020	2.2						
Biscuitroot phenology (index)				1.1	0.26	19.7			
Osmorhiza phenology (index)							0.064†	0.026	3.6
Vegetation features									
Shrub ground cover (%)	0.44†	0.18	4.0						
Total vegetation ground cover (%)				-0.14	0.046	12.8§			
$\ln([Total\ veg.\ ground\ cover] + 1)$				2.2	0.79				
Graminoid ground cover (%)	0.42†	0.25	14.8				1.3†	0.41	13.2
Total forest basal area (m ² /ha)	-0.49†	0.16	8.0	-1.2†	0.25	39.2	0.058	0.019	7.6
Elevation (m)	$-5.4 \times 10^{-7}†$	2.6×10^{-7}	2.8	0.0033	0.00095	11.0			
Weather									
Current month's temperature (°C)	0.21	0.062	11.0						
Cumulative growing season ppt. (cm)				0.13	0.06	2.4			
Total winter ppt. (cm)				-3.7†	1.2	10.2			
Gender (female)	0.49	0.26	2.0	-0.84	0.38	4.1			
Time									
Julian date							0.000074†	0.000025	8.9
Post-1988 fires							-1.3	0.45	8.7
Statistics									
χ^2 (df)	179	(1353)		116	(1343)		78	(1346)	
P	1.000			1.000			1.000		
R_L^2	0.91			0.94			0.96		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing all terms of the polynomials for this variable.

TABLE 14. Multiple regression models of the relations of number of excavations or number of plants per excavation for yampa, biscuitroot, or osmorhiza roots at a site where feeding on this food occurred, to food abundance, vegetation features, elevation, weather, age class of bear, and date for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Yampa (# of excavations) [†]			Yampa (# of plants/excavation) [†]			Biscuitroots (# of excavations) [†]			Osmorhiza (# of excavations) [†]		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-6.8	2.4		-4.1	0.91		1.5	2.0		2.8	0.29	
Yampa abundance (index)	0.17 [‡]	0.045	3.7									
Vegetation features												
Total basal area of dead trees (m ² /ha)				0.39	0.044	10.9§						
ln ([total basal area of dead trees] + 1)				-1.7	0.18							
Shrub ground cover (%)				-0.13 [‡]	0.021	7.7						
Graminoid ground cover (%)				0.48 [†]	0.072	6.1§	-1.9 [†]	0.75	0.5			
Graminoid ground cover (%) [‡]				-0.00070	0.00010							
Forb ground cover (%)							-0.0063 [‡]	0.0018	2.7			
Total vegetation ground cover (%)							0.12	0.051	0.1			
Elevation							0.0021	0.00067	1.7			
Weather												
Cumulative growing season ppt. (cm)	2.0 [†]	0.57	2.5	0.57 [†]	0.075	11.4				0.038 [‡]	0.011	1.7
Current month's ppt. (cm)												
Age (adult)				-0.30	0.062	4.7						
Julian date	0.024	0.0058	4.3	0.60 [†]	0.15	2.3						
Statistics												
F (num. df / den. df)	8.4	(3 / 44)		18.2	(8 / 16)		5.5	(4 / 51)		12.1	(1 / 27)	
P	0.000			0.000			0.001			0.002		
R ²	0.36			0.90			0.30			0.31		

[†]Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as ln [(x, y) + 1].

[‡]Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for this variable.

cover intermediate (Figs. 13a, 14a, & 14b). Given proximal effects, males were more likely than females to dig biscuitroots. Total numbers of excavations for biscuitroot also were greatest at higher elevations as well as on sites with intermediate total vegetation cover consisting of comparatively few forbs and graminoids (Table 14; Fig. 13d).

Osmorhiza roots were more likely dug by bears late in the growing season and in areas with extensive mesic subalpine fir forests or high-elevation elk winter range (Table 12; Fig. 15c). Osmorhiza roots were less likely dug when whitebark pine cone crops were large (Fig. 15a) and in areas with extensive low-elevation lodgepole pine forests. Proximal site features screened out the effects of cone crop size and the extent of subalpine fir forests and elk winter range (Table 13). Osmorhiza roots were more likely dug where osmorhiza was abundant and phenologically advanced and on sites with extensive graminoid ground cover (Figs. 13a & 14c). Unlike yampa and biscuitroots, the likelihood that osmorhiza had been dug increased with total forest basal area. Total number of excavations for osmorhiza at a given feeding site was greater during wet compared to dry months (Table 14; Fig. 12d).

Use of high-quality grazed foods

Graminoids were more often grazed in Spring and Estrus during years when ungulate carcasses and live elk were abundant (Fig. 16b) and in areas with extensive high-elevation elk winter range (Table 15). This type of grazing was less common following years when large whitebark pine cone crops were produced and in areas where and during years when bison were abundant. Grazing intensity, as betokened by the probability of finding a feces at the grazing site, also was lower in areas with extensive bison winter range as well as during years when carcasses were abundant (Table 17). Additionally, early season grazing of graminoids was uncommon during dry years and with warming seasonal temperatures (Fig. 16c), but increased following the fires of 1988. Proximal vegetation features screened out the effects of weather, winter range types, and the fires of 1988 (Table 16). Early-season grazing of graminoids was more likely on sites where forbs and graminoids were abundant, especially if the graminoids consisted of sedges (*Carex* spp.) and pre-flower bluegrasses (*Poa* spp.; Figs. 17b & 17c). Grazing intensity also peaked on sites where sedges were abundant, as well as where bluegrasses were pre-flower and shrub cover sparse (Table 17). Although the likelihood of finding any feces at sites where graminoids had been grazed was lower for

Osmorhiza

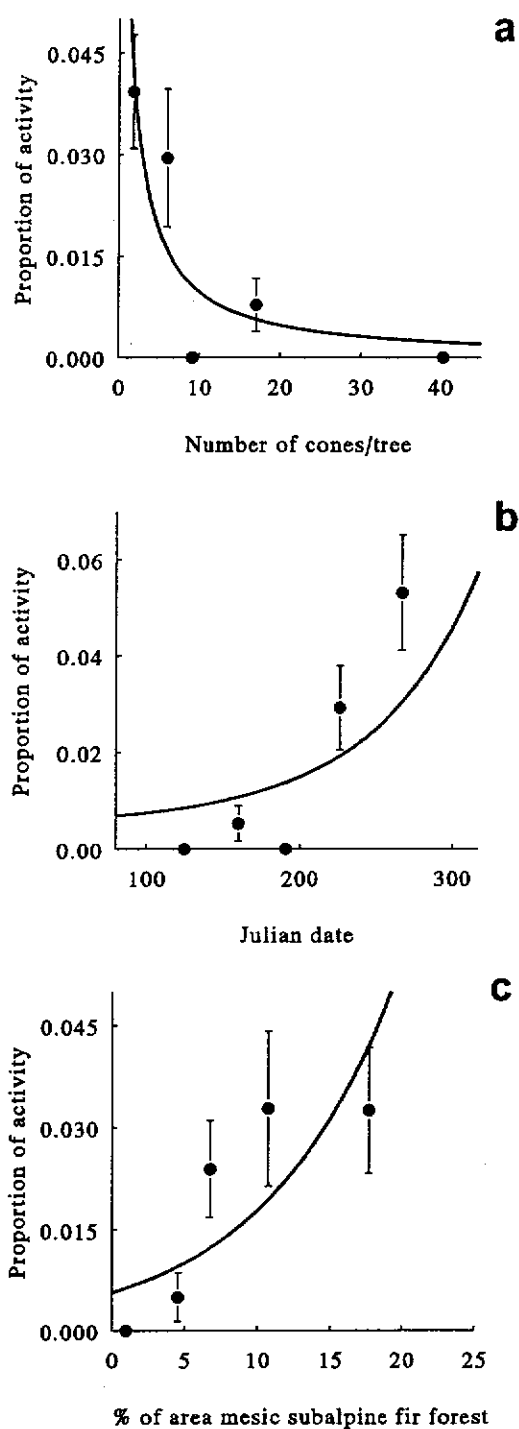


FIG. 15. Relations between grizzly bear use of osmorhiza roots in the Yellowstone ecosystem, 1977-92, and variables denoting effects of (a) the size of the whitebark pine cone crop, (b) date, and (c) extent of mesic subalpine fir forests in the surrounding BMU. Bear use is signified as the proportion of total activity involving osmorhiza roots. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

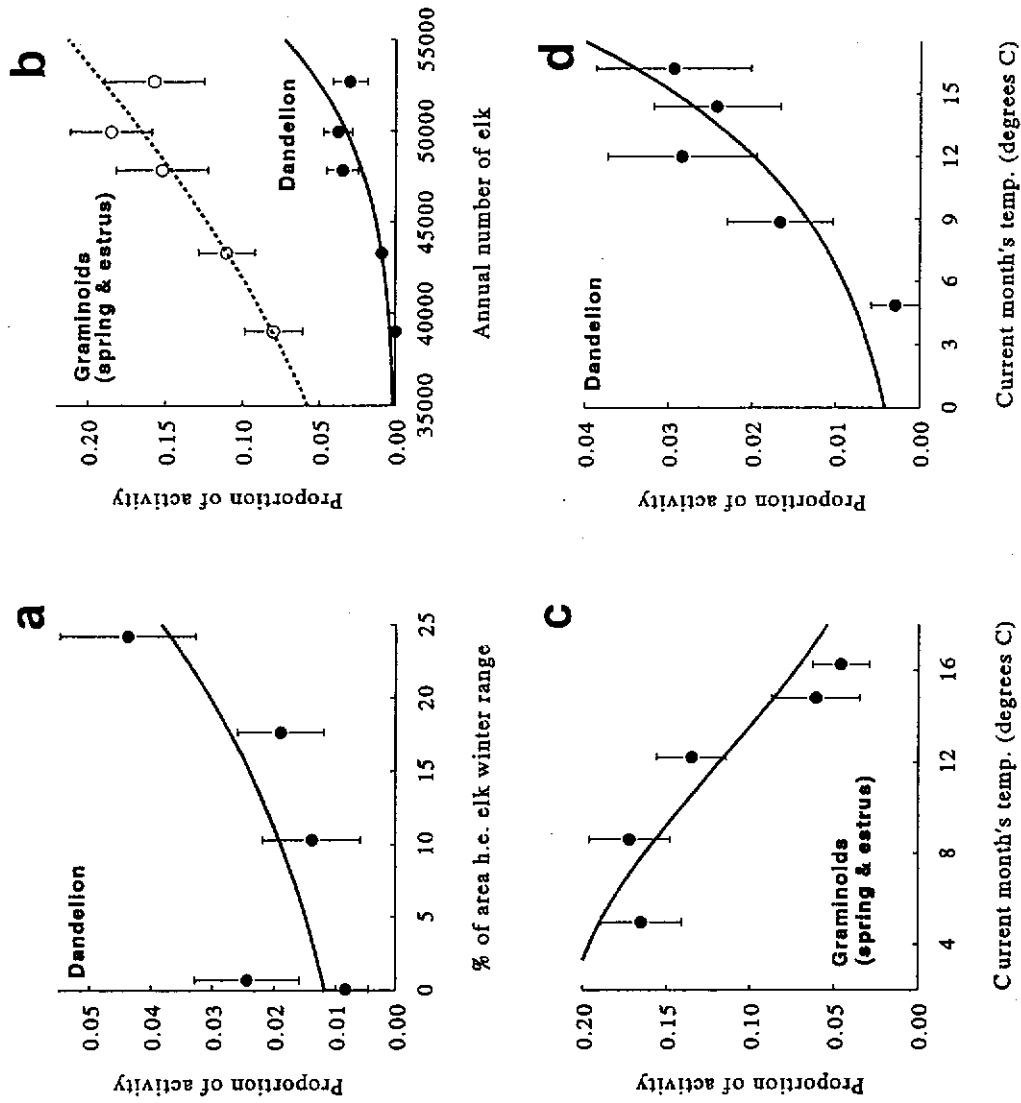


FIG. 16. Relations between grizzly bear grazing of clover, dandelions, and early-season graminoids in the Yellowstone ecosystem, 1977-92, and variables denoting effects of the extent of ungulate winter range in the surrounding BMU, elk numbers, and weather. Bear use is signified as the proportion of total activity involving these grazed foods. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 15. Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (spring or estrus), clover, or dandelions, related to variables pertaining to distal effects including food availability, extent of habitat types, weather, type of bear, and time, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Graminoids (Spring & Estrus)			Clover			Dandelion		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-153	30		-3.3	1.0		-108	33	
Food availability									
# of ungulate carcasses	0.000012‡	4.3×10^{-6}	15.2	-0.67†	0.19	12.2			
# of elk	17.7†	3.6	32.5				10.4†	2.9	15.6
# of bison	-4.8†	1.2	15.2						
# of whitebark pine cones (n/tree), previous year	-0.30†	0.15	1.9						
Extent of habitat types (% by BMU)									
Mesic non-forest				-0.014‡	0.0040	20.6			
Mesic subalpine fir				0.12	0.049	4.9			
Mesic Douglas-fir							-0.0053‡	0.0019	8.3
Bison winter range	-0.20†	0.11	1.6						
Low-elevation elk winter range				0.95†	0.28	13.8			
High-elevation elk winter range	0.25†	0.084	7.4				0.087	0.021	16.8
Weather									
Current month's temperature (°C)	-0.0090‡	0.0015	38.0				0.26	0.080	12.5
Cumulative growing season ppt. (cm)	-0.0030‡	0.0011	9.2						
Current month's ppt. (cm)							1.4†	0.40	10.3
Age (adult)							-0.32	0.18	1.1
Time									
Julian date							-2.6†	1.3	3.1
Post-1988 fires	0.90	0.26	11.4						
Statistics									
χ^2 (df)	222	(228)		68	(135)		255	(1503)	
P	0.594			1.000			1.000		
R_L^2	0.50			0.91			0.88		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

TABLE 16. Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (spring or estrus), clover, or dandelions, related to variables pertaining to distal and proximal effects, including availability of high-quality foods, extent of habitat types, food abundance, vegetation features, and time, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Graminoids (Spring & Estrus)			Clover			Dandelion		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-136	30		2.5	2.7		-15	3.5	
Food availability in ecosystem									
# of whitebark pine cones (n/tree), previous year	0.00051†	0.00020	4.0						
# of ungulate carcasses	0.00002	4.8×10^{-6}	16.3	-0.76†	0.30	5.4			
# of elk	12†	2.8	24.9				0.00019	0.00007	6.7
# of bison				-0.0020	0.0076	5.0			
Extent of habitat types (% of BMU)									
Low-elevation elk winter range				0.10	0.0047	3.2			
High-elevation elk winter range				-0.98†	0.40	6.7	0.0017†	0.00077	3.1
Wet non-forest				-2.6†	1.1	3.8			
Food abundance & phenology									
<i>Poa</i> spp. abundance (index)	0.082†	0.027	6.9						
<i>Carex</i> spp. abundance (index)	0.62†	0.22	6.3						
<i>Calamagrostis</i> spp. abundance (index)				1.2†	0.56	5.5			
Clover abundance (index)				0.62†	0.0954	147			
Dandelion abundance (index)							0.20†	0.036	29.7
<i>Poa</i> phenology (index)	1.2	0.42	9.0§						
<i>Poa</i> phenology (index) ²	-0.45	0.14							
Vegetation features									
Forb ground cover (%)	0.047	0.011	17.0				0.037	0.014	4.3
Graminoid ground cover (%)	0.61†	0.18	10.0				0.020	0.011	4.5
Shrub ground cover (%)							-0.57†	0.22	5.8
Amount of woody debris (index)	-0.44†	0.21	2.5						
Dead forest basal area (m ² /ha)							0.036	0.013	5.2
Julian date	-0.00007†	0.00002	9.7						
Statistics									
χ^2 (df)	393	(729)		52.3	(165)		210	(1298)	
P	1.000			1.000			1.000		
R_L^2	0.62			0.96			0.89		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for this variable.

TABLE 17. Logistic or multiple regression models of the relations of number of feces observed at a site where feeding on clover or dandelion occurred or of the probability that a feces had been present at a site where grazing on early season graminoids had occurred, to number of ungulate carcasses, extent of bison winter range, food abundance and phenology, vegetation features, weather, type of bear, and time, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Graminoids (Spring & Estrus) (Prob. of a feces being present)			Clover (# of feces)†			Dandelion (# of feces)†		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	2.4	0.97		-1.5	0.95		1.1	0.18	
# of ungulate carcasses in ecosystem	-0.00002‡	7.5×10^{-6}	8.8						
Bison winter range (% of BMU)	-0.69†	0.27	15.5						
Food abundance & phenology									
<i>Carex</i> spp. abundance (index)	1.1†	0.48	2.6						
<i>Poa</i> phenology (index)	-0.25‡	0.11	3.6						
Vegetation features									
Shrub ground cover (%)	-0.18	0.074	9.1						
Total basal area (m ² /ha)							0.015	0.0067	3.5§
ln([Total basal area] + 1)							-0.43	0.10	
Reproductive status — wt. COY	-1.8	0.54	4.9						
Julian date				0.013	0.0047	0.64			
Statistics									
χ^2 (df) or F (num. df / den. df)	76	(73)		7.9	(1 / 20)		11.6	(2 / 32)	
P	0.385			0.011			0.002		
R_L^2 or R^2	0.29			0.28			0.42		

†Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as $\ln([x, y] + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for this variable.

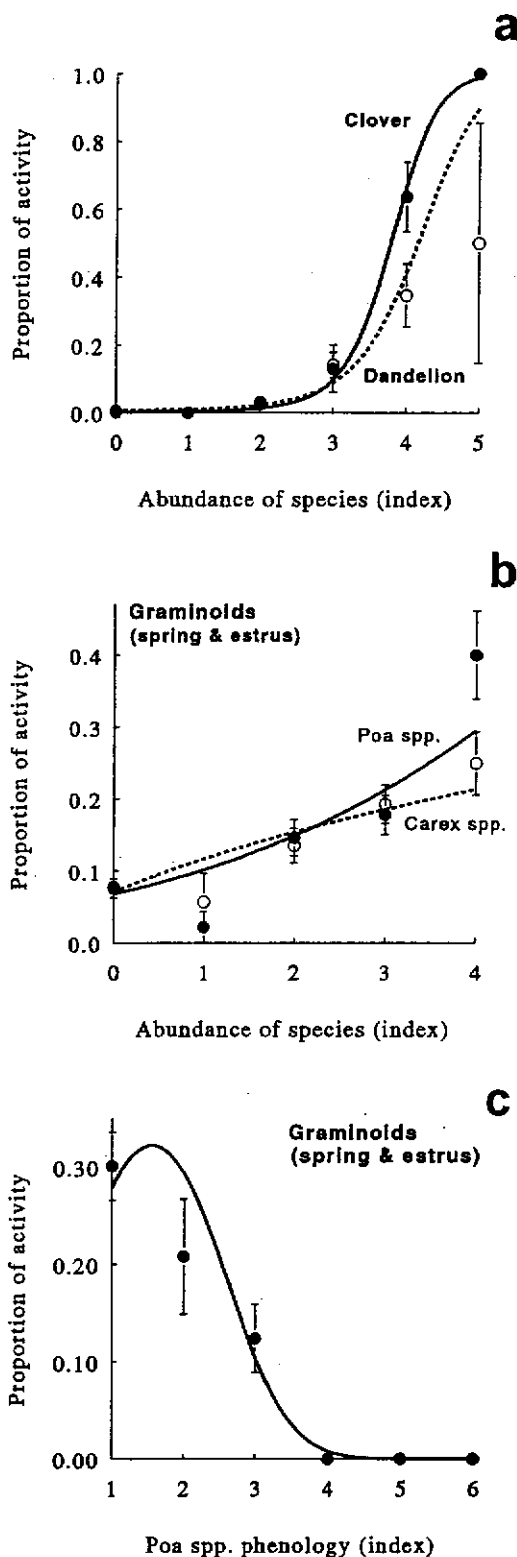


FIG. 17. Relations between grizzly bear grazing of clover, dandelion and early-season graminoids in the Yellowstone ecosystem, 1977-92, and variables denoting effects of species abundance and phenology. Bear use is signified as the proportion of total activity involving use of the indicated species. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

locations of females with COY compared to other bears (Table 17), when found, there were more likely to be ≥ 2 feces ($\text{logit}[p] = -1.3 - 0.79[\text{wt. COY}]; R^2_L = 0.44, \Delta = 74$).

Clover was grazed by grizzly bears more often in areas with extensive mesic subalpine forest habitats or low-elevation elk winter ranges (Table 15). Clover grazing was less common during years when ungulate carrion was abundant during Spring, as well as in areas with extensive mesic non-forest areas. Proximally, clover grazing was markedly more likely where clover was abundant (Table 16; Fig. 17a). Considering the proximal effects of clover abundance, bears were less likely to graze it during years when bison were abundant and in areas with extensive wet non-forest habitats. As betokened by number of feces, grazing intensity increased as the growing season progressed (Table 17).

In common with clover and early season graminoids, dandelions were grazed more often during years when elk were abundant or in areas with extensive elk winter range (Table 15; Figs. 16a & 16b). In addition, dandelions were grazed more often during the warmest wettest months (Fig. 16d) and less often in areas with extensive mesic Douglas-fir forests. Grazing of dandelions declined as the growing season progressed and was less likely to occur if the located bear were an adult. Proximal features screened out the effects of weather, date, type-of-bear, and Douglas-fir habitats (Table 16). Grazing was more likely where dandelions, graminoids, other forbs, and coarse woody debris were abundant and where there were few shrubs (Figs. 17a). Intensity of grazing on dandelions peaked at intermediate levels of forest basal area (Table 17).

Use of fibrous vegetal foods

Graminoids were grazed by grizzly bears during Hyperphagia more often in areas with extensive bison winter ranges and during years when elk and whitebark pine cones were abundant (Table 18; Fig. 18a). Otherwise, this type of grazing declined after the fires of 1988. Proximally, late-season grazing of graminoids was more common on sites with extensive vegetation ground cover that included abundant timothy (*Phleum* spp.) and reedgrasses (*Calamagrostis* spp.) but few shrubs and wheatgrasses (*Agropyron* spp.; Table 19; Figs. 19a & 19d). Likelihood of grazing also increased with nearness in the open to forest edges (Fig. 19e). Accounting for proximal effects, late season use of graminoids was more likely in areas with extensive whortleberry-type and low-elevation spruce forests and less likely in areas with extensive high-elevation elk winter range. As betokened by number

TABLE 18. Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (Hyperphagia) or thistles related to variables pertaining to distal effects including food availability, the extent of habitat types, weather, age class of bear, and time period, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Graminoids (Hyperphagia)			Thistle		
	β_i	SE	Δ	β_i	SE	Δ
Constant	-113	23		34	17	
Food availability in ecosystem						
# of elk	10†	2.1	30.0	$5.4 \times 10^{-9}†$	1.8×10^{-9}	19.0
# of bison				-6.9†	2.7	11.1
# of whitebark pine cones (n/tree)	0.00064†	0.00026	3.6			
Extent of habitat types (% by BMU)						
Low-elevation elk winter range				-0.087	0.042	3.2
Bison winter range	0.0030†	0.0017	1.3			
Weather						
Current month's ppt. (cm)				0.018†	0.0086	1.6
Current month's temperature (°C)				0.013†	0.0043	10.6
Age (adult)				0.89	0.52	2.9
Post-1988 fires	-0.52	0.18	7.7			
Statistics						
χ^2 (df)	81.4	(83)		70.0	(457)	
P	0.528			1.000		
R_L^2	0.69			0.94		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

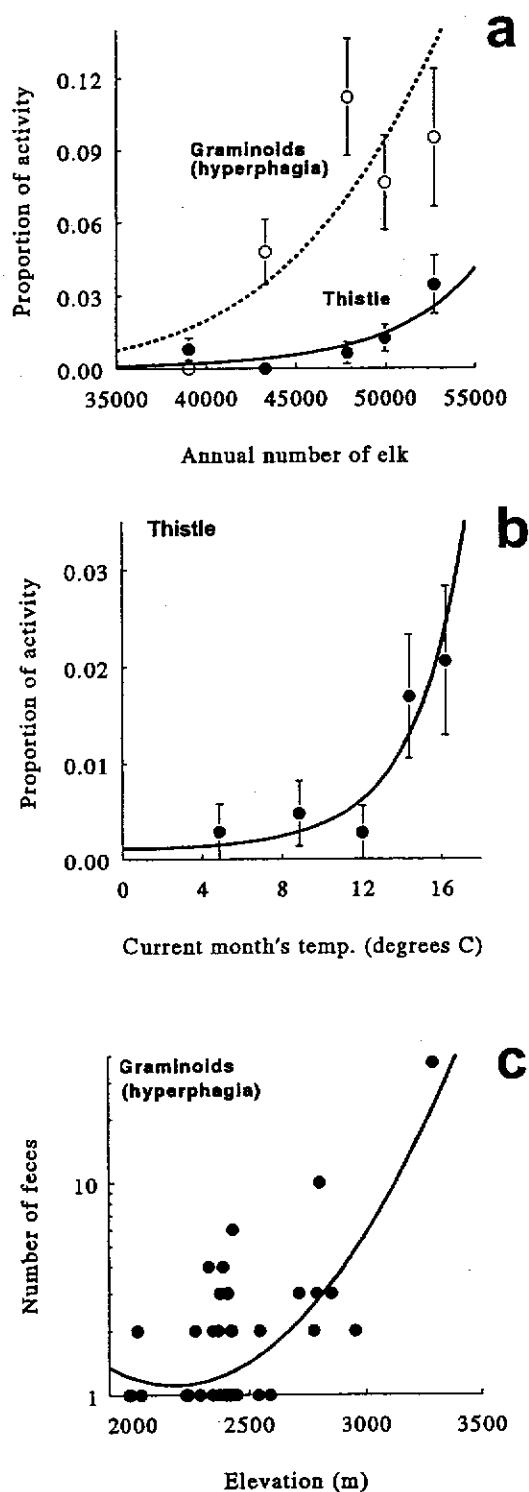


FIG. 18. Relations between grizzly bear grazing of fibrous foods in the Yellowstone ecosystem, 1977-92, and variables denoting effects of number of elk in the ecosystem, temperature, and elevation. Bear use is signified as either the proportion of total activity involving use of thistle or late-season graminoids or the number of feces found at a feeding site. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 19. Logistic regression models for the logit-transformed probability that a bear had been feeding on graminoids (hyperphagia) or thistles, related to variables pertaining to distal and proximal effects including food availability, the extent of habitat types, food abundance at the site, vegetation and site features, and weather, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Graminoids (Hyperphagia)			Thistle		
	β_i	SE	Δ	β_i	SE	Δ
Constant	-111	32		-22	5.1	
# of elk in ecosystem	10†	2.9	13.6	$4.4 \times 10^{-9}\ddagger$	1.5×10^{-9}	12.0
Extent of habitat types (% by BMU)						
High-elevation elk winter range	-0.0056†	0.0024	3.9			
Mesic non-forest	0.19	0.11	0.8			
Whortleberry-type forest	0.00065†	0.00028	3.4			
Low-elevation spruce forest	0.019†	0.0064	6.8			
Food abundance						
<i>Phleum</i> spp. abundance (index)	0.20†	0.054	12.2			
<i>Calamagrostis</i> spp. abundance (index)	0.11†	0.036	7.3			
<i>Agropyron</i> spp. abundance (index)	-0.75†	0.36	4.3			
Thistle abundance (index)				1.8	0.42	27.6
Slope (°)				-1.5†	0.66	4.0
Vegetation features						
Total forest basal area (m ² /ha)	-0.33†	0.14	5.2			
Dead basal area (m ² /ha)				0.0011	0.00043	0.9
Graminoid ground cover (%)				1.7†	0.63	10.5
Shrub ground cover (%)	-0.14	0.045	14.5			
Total vegetation ground cover (%)	0.00016†	0.000066	23.3			
Distance to forest edge (m)	-0.57†	0.13	19.5	-0.46†	0.25	1.9
Current month's temperature (°C)				0.019†	0.0064	10.2
Statistics						
χ^2 (df)	187	(599)		58.6	(1340)	
<i>P</i>	1.000			1.000		
R_L^2	0.79			0.97		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

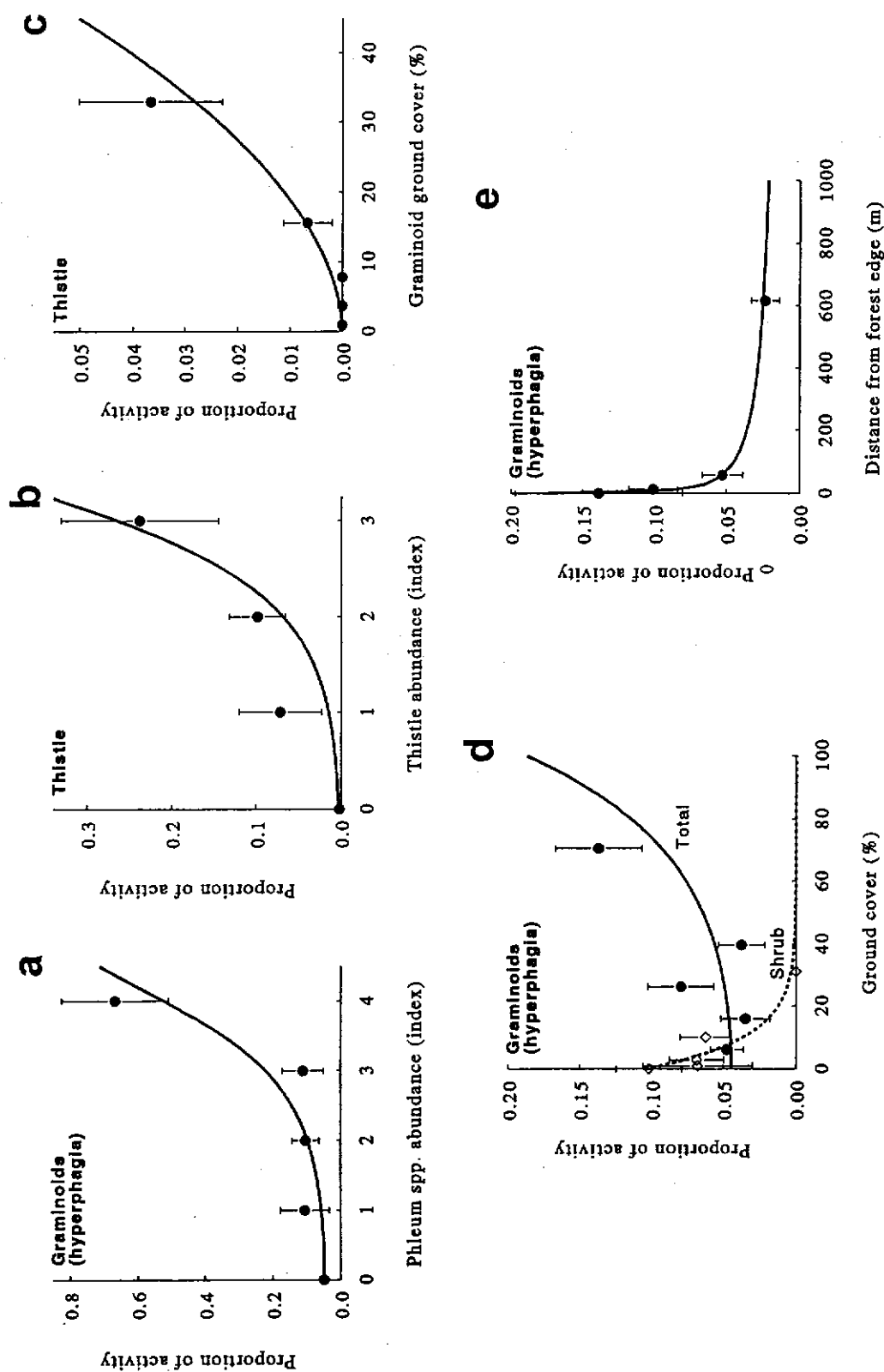


FIG. 19. Relations between grizzly bear grazing of fibrous foods in the Yellowstone ecosystem, 1977-92, and variables denoting effects of species abundance, vegetation cover, and distance to forest. Bear use is signified as the proportion of total activity involving use of thistle or late-season graminoids. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

of feces at a feeding site, grazing intensity tended to be greater at high elevations (Fig. 18c), during wet months, and where sedges were abundant (Table 20).

In common with dandelions and early-season graminoids, elk thistles (*Cirsium scariosum*) were grazed more often by grizzly bears during years when elk were most abundant (Table 18; Fig. 18a). Use of thistles also was more common during the wettest and warmest months (Fig. 18b) or when an adult bear was involved and less common during years when bison were most abundant and in areas with extensive low-elevation elk winter range. Proximally, the likelihood of thistle grazing was positively associated with thistle abundance, graminoid ground cover (Figs. 19b & 19c), and nearness to forest/non-forest edge (Table 19). Use of thistle also was more likely on gentle slopes and on forested sites with dead standing trees. Even so, intensity of thistle use – as betokened by the number of plants grazed at a site – peaked on non-forest sites (Table 20).

Use of ants

The likelihood that grizzly bears would use ants from hills of dirt and debris increased with monthly temperatures (Fig. 20c), but otherwise declined with progression of the growing season and was lower in areas with extensive mesic non-forest habitats (Table 21). Paradoxically, although use of ants from dirt and debris hills was more likely in areas with extensive ungulate winter ranges of all types, use was less common during years when bison were most abundant (Fig. 20b). Proximally, use of ants from hills was most likely on gentle slopes on sites with no trees (Table 21; Fig. 20d). By contrast, the sizes of excavations in individual anthills were largest on more heavily forested sites, far from forest/non-forest edges (Table 23). Given these proximal effects, bears were more likely to use ants from hills in areas with extensive recent burns and less likely to use them either after the 1988 fires or during wet growing seasons.

As with grizzly bear use of ants from hill, grizzly bear use of ants from logs increased with warming temperatures and was less likely in areas with extensive mesic non-forest habitats (Table 22; Figs. 20a & 20c). Unlike use of ants from hills, bear use of ants from logs increased with progression of the growing season (Fig. 20d). Otherwise, excavation of ants from logs was less common following or during years with large whitebark pine cone crops or in areas with extensive mesic subalpine fir forests and more common during years when ungulate carrion was abundant during Spring or in areas with extensive mesic Douglas-fir or

TABLE 20. Multiple regression models of the relations of number of feces observed or stems consumed at a site where feeding on either graminoids (Hyperphagia) or thistle occurred, to food abundance, vegetation and site features, and weather, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_1 refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Graminoids (Hyperphagia)		Thistle	
	(# of feces) \dagger		(# of stems) \dagger	
Constant	238	60	2.6	0.22
<i>Carex</i> spp. abundance (index)	0.025 \ddagger	0.013	1.6	
Vegetation & site features				
Total forest basal area (m ² /ha)			-0.54 \ddagger	0.12
Elevation (m)	0.016	0.0035	17.1	1.9
ln(Elevation)	-36	8.8		
Current month's ppt. (cm)	0.019 \ddagger	0.0055	5.9	
Statistics				
<i>F</i> (num. df / den. df)	18.6	(4 / 38)	20.2	(1 / 8)
<i>P</i>	0.000		0.002	
<i>R</i> ²	0.66		0.72	

\dagger Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as $\ln([x, y] + 1)$.

\ddagger Coefficient was estimated for squared values of the independent variable.

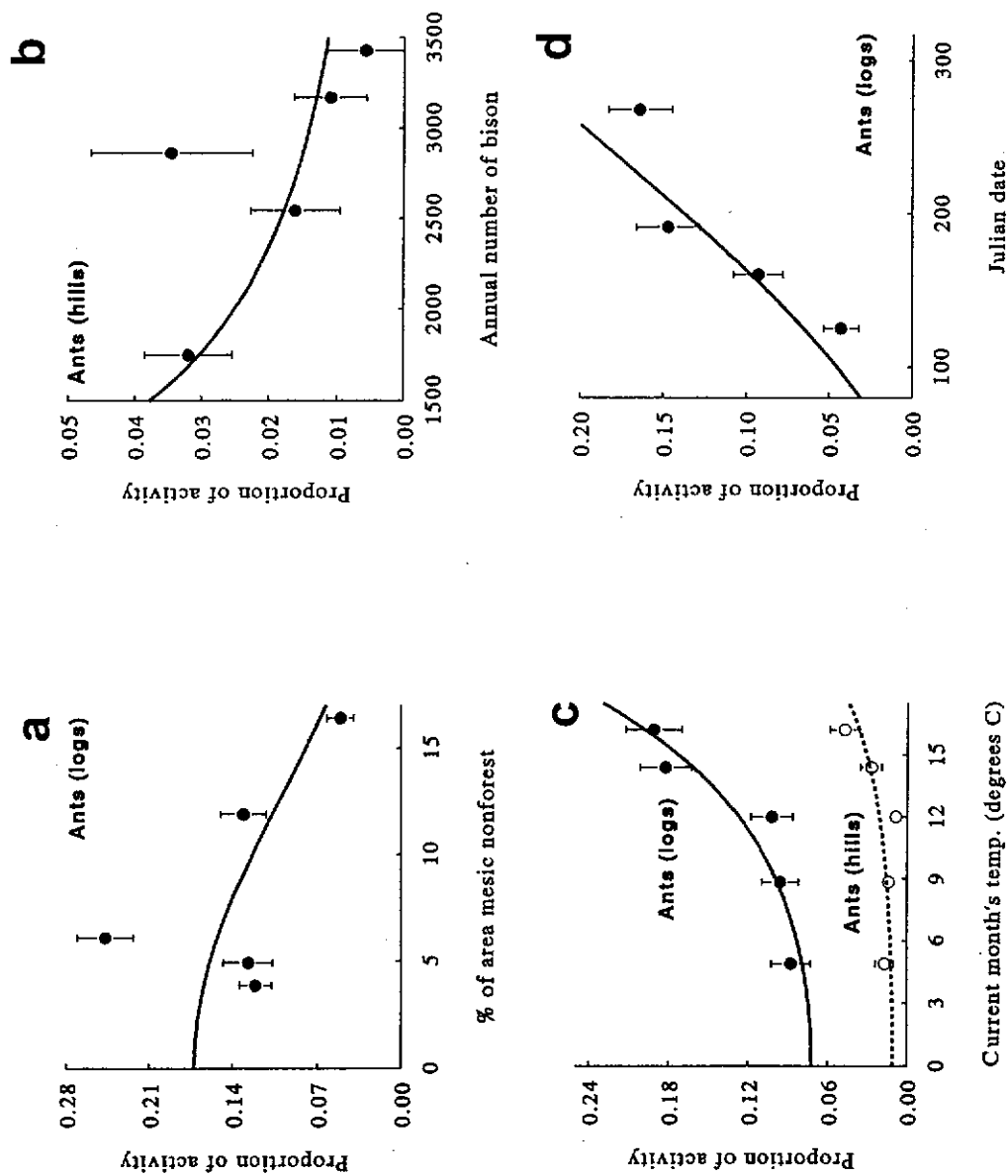


FIG. 20. Relations between grizzly bear use of ants from logs and hills in the Yellowstone ecosystem, 1977-92, and variables denoting effects of (a) extent of mesic non-forest in the surrounding BMU, (b) number of bison in ecosystem, (c) temperature, and (d) date. Bear use is signified as the proportion of total activity involving ants from logs. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 21. Logistic regression models for the logit-transformed probability that a bear had been feeding on ants in dirt/debris hills, related to variables pertaining to distal and proximal effects including extent of habitat types, vegetation and site features, weather, and time, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	11	3.4		9.3	5.0	
# of bison in ecosystem	-2.0†	0.46	15.9			
Extent of habitat types (% of BMU)						
Mesic non-forest	-0.35	0.11	11.9			
Low-elevation elk winter range	0.0028	0.0017	0.6			
High-elevation elk winter range	0.0062	0.0022	7.9			
Bison winter range	0.68†	0.26	7.3	0.086	0.036	4.1
Recently burned or harvested (dry)				0.71†	0.28	4.5
Slope (°)				-0.43†	0.19	3.4
Total forest basal area (m ² /ha)				-0.45†	0.14	36.7
Weather						
Current month's temperature (°C)	0.0089‡	0.0024	15.8	0.0083‡	0.0025	11.1
Cumulative growing season ppt. (cm)				-0.097	0.050	2.0
Time						
Julian date	-0.00003‡	0.000013	6.3	-2.8†	0.95	7.9
Post-1988 fires				-1.2	0.36	9.9
Statistics						
χ^2 (df)	286	(1362)		292	(1554)	
P	1.000			1.000		
R_L^2	0.87			0.87		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

TABLE 22. Logistic regression models for the logit-transformed probability that a bear had been feeding on ants in logs, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, vegetation and site features, weather, and time, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	-11	1.8		-12	2.4	
Food availability						
# of whitebark pine cones (n/tree)	-0.53†	0.094	28			
# of whitebark pine cones (n/tree), previous yr	-0.00084‡	0.00018	25	-0.00062‡	0.00019	11
# of ungulate carcasses	0.16†	0.087	19			
Extent of habitat types (% of BMU)						
Mesic non-forest	-0.0061‡	0.0011	31			
Low-elevation lodgepole pine forest	0.0035‡	0.00079	16	0.057	0.019	7
Mesic Douglas-fir forest	0.060	0.013	19			
Mesic subalpine fir forest	-0.035	0.012	7			
Recently burned or harvested (dry)				-0.029	0.011	6
Site habitat type --- Dry non-forest				-0.71	0.31	31
Mesic non-forest				-0.27		
Mesic forest				0.67	0.18	
Low-elevation forest				0.11	0.23	
High-elevation forest				0.20	0.18	
Site features						
Elevation (m)				-0.0015	0.00052	7
Slope (°)				-0.055	0.023	7§
ln(Slope + 1)				0.78	0.25	
Vegetation features						
Total forest basal area (m ² /ha) ²				-0.099†	0.023	31
Amount of woody debris (index)				1.6†	0.42	11§
Amount of woody debris (index) ²				-0.036	0.013	
Size of woody debris (index)				0.58	0.20	9§
ln([Size of woody debris] + 1)				-1.7	0.71	
Decomposition of woody debris (index)				0.29†	0.14	2
Current month's temperature (°C)	0.0039‡	0.00090	18	0.0050‡	0.0011	28
Julian date	1.8†	0.33	29	2.2†	0.41	20
Statistics						
χ^2 (df)	1026	(1337)		872	(1411)	
P	1.000			1.000		
R_L^2	0.50			0.56		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for this variable.

¶Coefficient was calculated by difference.

TABLE 23. Multiple regression models of the relations of number of excavations or mean size of excavation for ants in logs or hills at a site where feeding of this type occurred, to vegetation and site features, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Ants (logs) (# of excavations) [†]			Ants (logs) (dm ³ /excavation) [†]			Ants (hills) (dm ³ /excavation) [†]		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	0.74	0.094		4.0	0.26		0.74	0.40	
Amount of deadfall (index)	0.15†	0.067	0.13						
Distance from/into forest (m)				-0.14†	0.055	0.52	0.21†	0.081	0.20
Graminoid ground cover (%)				-0.00025‡	0.00011	0.74			
Total forest basal area (m ² /ha)							0.36†	0.12	0.89
Statistics									
<i>F</i> (num. df / den. df)	5.1	(1 / 165)		4.7	(2 / 143)		6.5	(2 / 21)	
<i>P</i>	0.025			0.011				0.006	
<i>R</i> ²	0.03			0.06				0.38	

†Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as $\ln ([x, y] + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

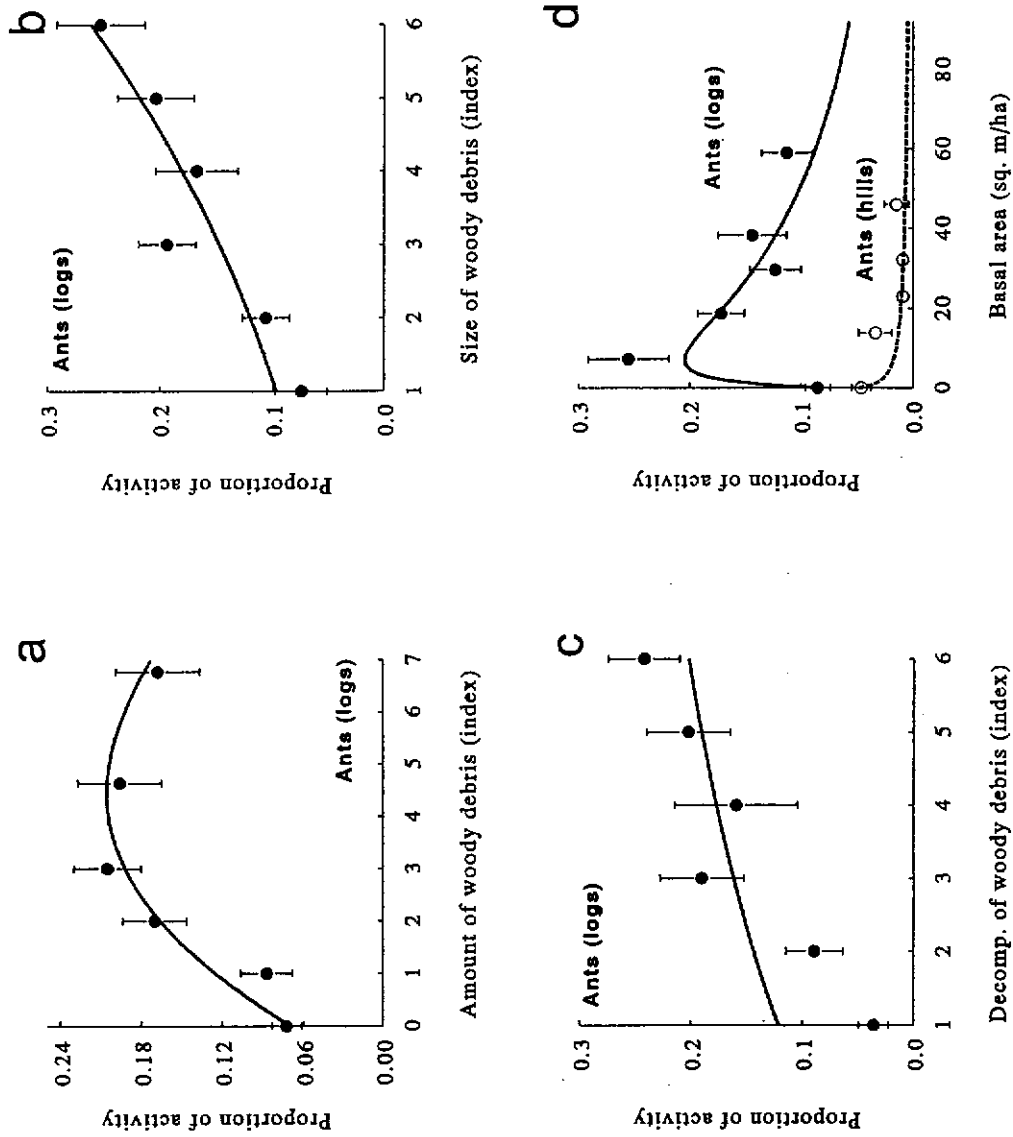


FIG. 21. Relations between grizzly bear use of ants in logs and hills in the Yellowstone ecosystem, 1977-92, and variables denoting effects of forest structure. Bear use is signified as the proportion of total activity involving use of ants at a feeding site. Points bracketed by standard error bars are proportions for quintiles, sextiles, or septiles shown to illustrate goodness-of-fit.

low-elevation lodgepole pine forests. The proximal effects of forest structure screened out the distal effects of most habitat types as well as ungulate carrion and current year whitebark pine cone crops. Proximally, use of ants from logs was most likely with intermediate amounts of large diameter, well-decomposed, coarse woody debris under a sparse to moderately open forest overstory (Table 22; Fig. 21). Use also was more likely on moderate slopes at low elevations. As might be expected, total number of logs dug by a bear at a given site increased with the amount of coarse woody debris (Table 23). The size of excavations in individual logs were larger where logs were closer to forest/nonforest edge and on sites with sparse graminoid ground cover (Table 23).

Use of rodents and rodent food caches

Grizzly bears excavated rodents or their food caches during Spring and Estrus more often in areas with extensive wet non-forest habitats or bison winter range and following comparatively dry winters (Table 24; Fig. 22d). Early-season use of rodents was less likely as the summer progressed (Fig. 22e) and following the 1988 fires. Given proximal effects, and complementary to the positive effect of bison winter range, bears were more likely to dig for rodents during years when bison were most abundant. Proximally, grizzly bears were more likely to have dug for rodents where they had been located on a mesic or wet non-forest site where yampa was abundant (Table 24; Fig. 22a). The size of excavations also was larger where yampa was more abundant as well as where a subadult bear had been involved (Table 25). On the other hand, likelihood of use declined as amount of forest basal area and coarse woody debris increased (Fig. 22b). Overall, grizzly bears were most successful at finding rodent nests on steeper slopes (Fig. 22c) and rodent food caches on sites with extensive vegetation cover consisting of few forbs and sedges (Table 25).

Grizzly bears were more likely to excavate rodents or rodent food caches during Hyperphagia during wet months, although that likelihood declined during years of greater cumulative growing season ppt (Table 26). Otherwise, late-season use of rodents was more likely on sites with intermediate amounts of coarse woody debris and abundant graminoids that included wheatgrass (Table 26; Figs. 23a & 23b). Considering proximal effects, and contrary to what was observed for early-season use of rodents, late-season use of rodents declined after the 1988 fires. Excavations were larger at a given site on gentle slopes where there were abundant sedges (Table 27; Fig. 23c). In keeping with the positive association of

TABLE 24. Logistic regression models for the logit-transformed probability that a bear had been feeding on rodents or rodent food caches during Spring and Estrus, related to variables pertaining to distal and proximal effects including number of bison, extent of habitat types, location within a habitat type, vegetation features, winter ppt, and time, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to the change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	2.9	1.7		-23	6.3	
# of bison in ecosystem				2.8†	0.82	11.8
Extent of habitat types (% of BMU)						
Wet non-forest	1.1†	0.53	2.8			
Low-elevation elk winter range				-0.052	0.028	1.3
Bison winter range	0.057	0.024	3.6	0.060	0.034	1.2
Proximal effect of habitat type						13.6
Dry non-forest				0.32	0.33	
Mesic/wet non-forest				0.87§		
Mesic forest				-0.44	0.53	
Low-elevation forest				-0.20	0.42	
High-elevation forest				-0.56	0.46	
Abundance of yampa at site (index)				0.13†	0.046	12.5
Vegetation features						
Total forest basal area (m ² /ha)				-0.37†	0.15	16.3
Amount of woody debris (index)				-0.061†	0.036	3.3
Total winter ppt. (cm)	-1.2†	0.39	8.0			
Time						
Post-1988 fires	-0.45	0.15	7.6	-0.85	0.23	13.2
Julian date	-0.019	0.0045	15.0	-0.00007‡	0.00002	9.7
Statistics						
χ^2 (df)	413	(734)		306	(778)	
P	1.000			1.000		
R_L^2	0.66			0.73		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§Coefficient was calculated as the difference of the other summed coefficients from 0, for “proximal effect of habitat type” only.

Rodents (Spring & Estrus)

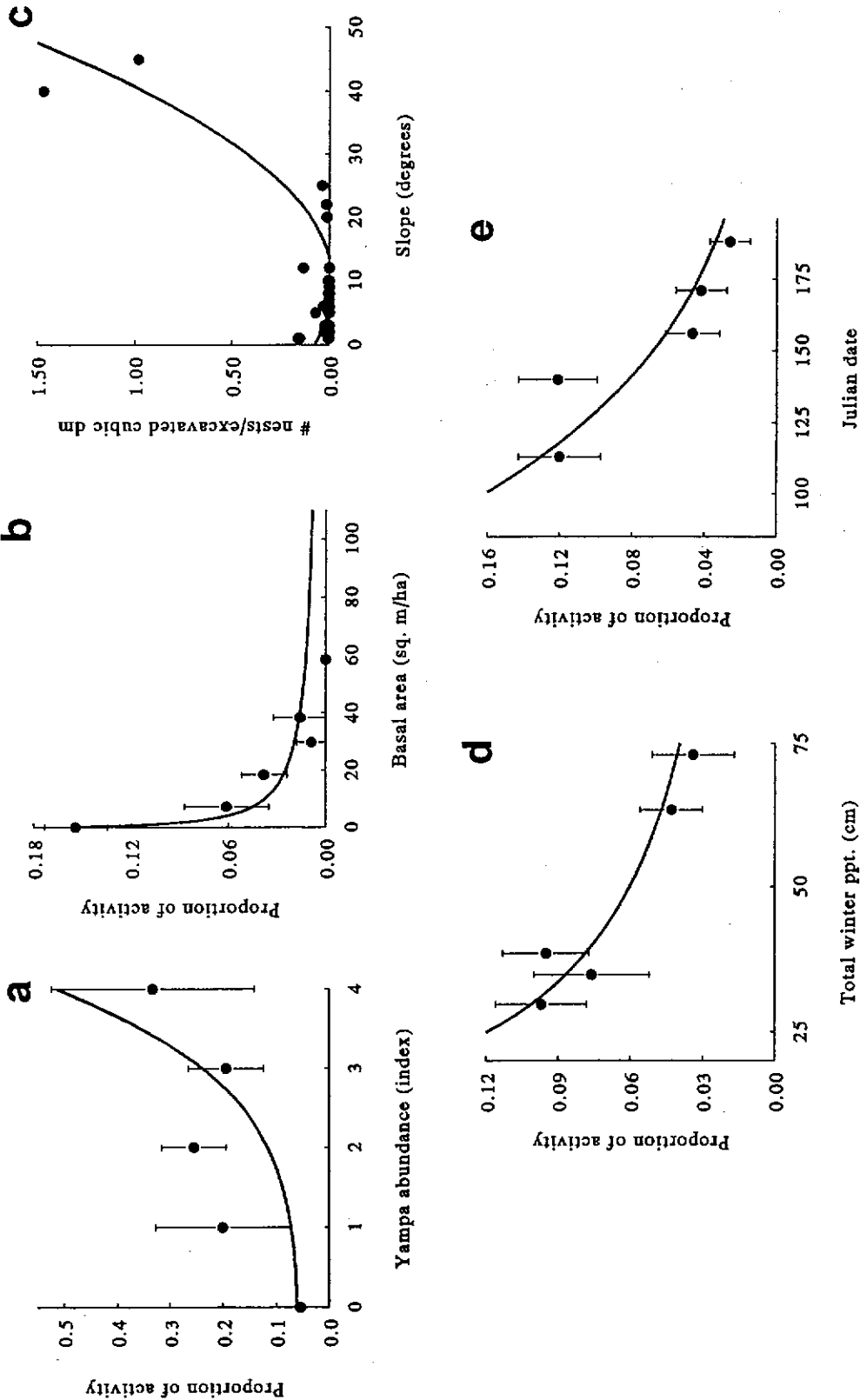


FIG. 22. Relations between grizzly bear use of rodents or rodent food caches during Spring and Estrus in the Yellowstone ecosystem, 1977-92, and variables denoting effects of vegetation features, slope, winter ppt, and date. Bear use is signified as either the proportion of total activity involving use of rodents or the number of rodent nests encountered per unit volume of excavation. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 25. Multiple regression models of the relations of volume of excavations for rodents or number of nests or root caches per unit volume of excavation at a site where feeding on rodents occurred during Spring or Estrus, to species abundance, vegetation and site features, and age-class of bear, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	dm ³ of excavations†			# of nests/dm ³ of excavations†			# of caches/dm ³ of excavations†		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	5.6	0.62		0.29	0.087		0.0022	0.013	
Species abundance									
Yampa abundance (index)	1.5†	0.43	6.3						
<i>Carex</i> spp. abundance (index)							-0.0092†	0.0038	1.0
Vegetation and site features									
Forb ground cover (%)							-0.015†	0.0041	2.8
Total vegetation ground cover (%)							0.016†	0.0055	0.7
Slope (°)				0.045	0.0052	19.3			
ln(Slope)				-0.31	0.066				
Age (adult)	-1.9	0.67	1.1						
Statistics									
<i>F</i> (num. df / den. df)	9.7	(2 / 38)		62.2	(2 / 32)		8.5	(3 / 23)	
<i>P</i>	0.000			0.000			0.000		
<i>R</i> ²	0.34			0.80			0.53		

†Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as $\ln([x, y] + 1)$.

TABLE 26. Logistic regression models for the logit-transformed probability that a bear had been feeding on rodents or rodent food caches during Hyperphagia, related to variables pertaining to distal and proximal effects including location within a habitat type, vegetation features, weather, and time period, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	-1.2	0.62		-1.8	0.93	
Abundance of <i>Agropyron</i> spp. at site (index)				0.093†	0.035	5.7
Vegetation features						
Amount of woody debris (index)				0.41	0.20	7.9§
$\ln([\text{Amount of woody debris}] + 1)$				-2.1	0.67	
Graminoid ground cover (%)				0.038	0.011	5.4
Weather						
Cumulative growing season ppt. (cm)	-1.8†	0.59	7.6	-0.89†	0.43	2.2
Current month's ppt. (cm)	1.3†	0.59	3.0			
Post-1988 fires				0.62	0.24	5.7
Statistics						
χ^2 (df)	70	(49)		178	(541)	
P	0.026			1.000		
R_L^2	0.71			0.79		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was calculated as the difference of the other summed coefficients from 0, for "proximal effect of habitat type" only.

§This Δ value includes the effects of removing both terms of the polynomial for this variable.

Rodents (Hyperphagia)

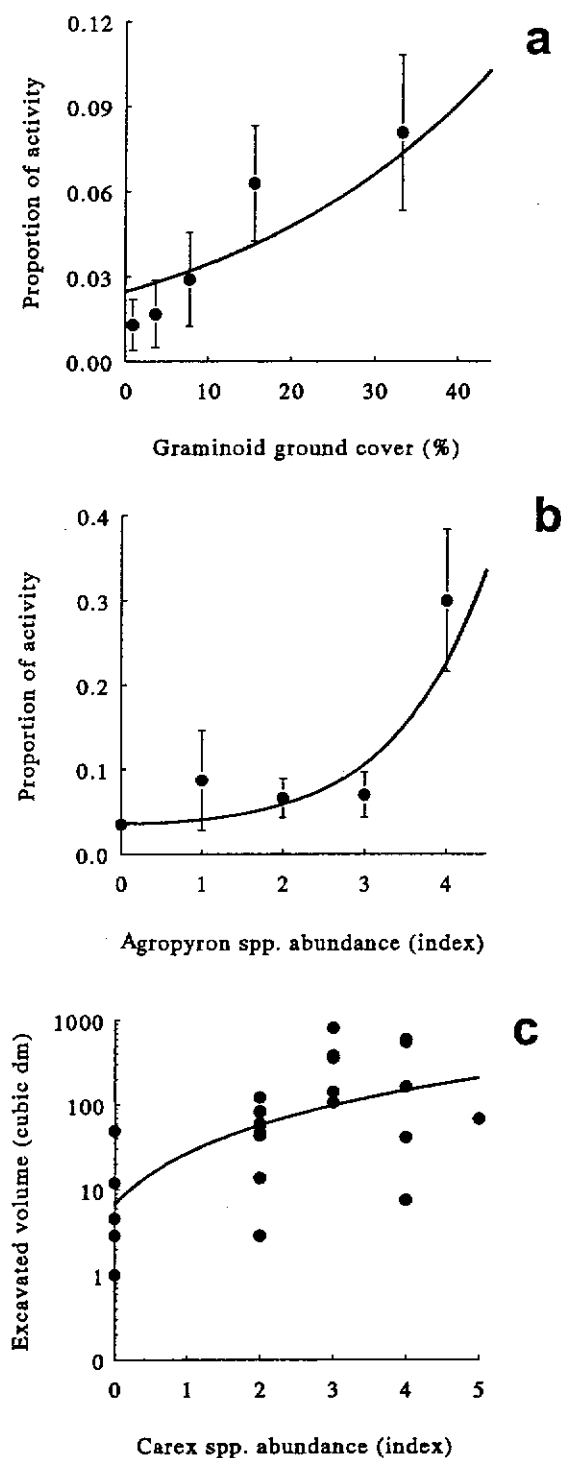


FIG. 23. Relations between grizzly bear use of rodents or rodent food caches during Hyperphagia in the Yellowstone ecosystem, 1977-92, and variables denoting effects of graminoid cover and species abundance. Bear use is signified as either the proportion of total activity involving use of rodents or the total volumes of excavations for rodents at a feeding site. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 27. Multiple regression models of the relations of volume of excavations for rodents or number of nests or root caches per unit volume of excavation at a site where feeding on rodents occurred during Hyperphagia, to species abundance and slope, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	dm ³ of excavations†			# of nests/dm ³ of excavations†			# of caches/dm ³ of excavations†		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	4.2	0.76		0.0067	0.0059		-0.0010	0.0033	
Species abundance at site									
<i>Carex</i> spp. abundance (index)	1.8†	0.37	4.8						
<i>Agropyron</i> spp. abundance (index)				0.0024‡	0.00080	0.91	0.0017‡	0.00043	2.6
<i>Melica spectabilis</i> abundance (index)				-0.017†	0.0066	0.07	-0.017†	0.0065	0
Slope (°)	-1.2†	0.35	1.9						
Statistics									
F (num. df / den. df)	17.4	(2 / 21)		5.3	(2 / 19)		7.9	(2 / 17)	
P	0.000			0.015			0.004		
R ²	0.62			0.36			0.48		

†Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as $\ln([x, y] + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

wheatgrass with likelihood of use, grizzly bears were most successful at finding both rodent nests and rodent food caches where wheatgrass was abundant and onion grass (*Melica spectabilis*) uncommon (Table 27).

Use of mushrooms

The likelihood that grizzly bears would use mushrooms increased with summer warmth and time-of-year (Fig. 24b) and was greatest in areas with extensive low-elevation lodgepole pine forests, extensive low-elevation elk winter range, and during years when elk populations were at intermediate levels (Table 28; Fig. 24a). Use of mushrooms was least likely in areas with extensive whitebark pine forests (Fig. 24a). However, likelihood of use increased during years when whitebark pine cone crops were large, at the same time that the extent of excavations at a given feeding site declined (Table 28). Forest structure screened out the effects of temperature and whitebark pine cone crops. Proximally, grizzly bears were most likely to excavate mushrooms in forests with substantial amounts of lodgepole or whitebark pines (Fig. 24c), few dead trees, and sparse vegetation ground cover (Fig. 24d). Otherwise, adult bears were more likely to use mushrooms than were subadults.

Use of berries

Consumption of berries by grizzly bears in the Yellowstone area was rare. When use of berries did occur it was more likely later in the growing season, in areas with extensive mesic Douglas-fir habitat types, and if the bear was male (Table 29). Likelihood of use was lowest in areas with extensive high-elevation elk winter range and during years when bison were most abundant. Proximally, consumption of berries was most likely during a cooler growing season month where shrub cover was extensive and comprised mostly of sheperdia (*Sheperdia canadensis*).

Bedding

Grizzly bears were most likely to excavate and use beds following wet winters, during wet months, or when large whitebark pine cone crops were produced (Table 30). Likelihood of bedding declined with time-of-year, and was lowest during years with cumulatively wet growing seasons or abundant ungulate carrion during Spring. Otherwise, bedding was uncommon in areas with extensive recent burns or mesic non-forest habitats and common in areas with extensive high-elevation elk winter range. Bears that were alone tended to bed more often than females accompanied by COY (Fig. 25c). Proximally, bedding was more

TABLE 28. Multiple regression models of relations of the logit-transformed probability that a bear had been feeding on mushrooms or of number of excavations for mushrooms at a site where this feeding occurred, to food abundance, extent of habitat types, vegetation and site features, weather, type of bear, and time, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Probability of use (distal effects only)			Probability of use (distal & proximal effects)			# of excavations†		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-36	8.2		-2744	876		3.4	0.24	
Food availability in ecosystem									
# of whitebark pine cones	0.00033‡	0.00019	0.7				-0.00065‡	0.00023	0.87
# of elk				-0.0060	0.0020	9.9§			
ln(# of elk)				279	90				
Extent of habitat types (% of									
Whitebark pine forest	-0.16	0.034	27.3						
Low-elevation elk winter range				0.50†	0.30	1.2			
Low-elevation lodgepole pine				1.5†	0.42	20.6			
Slope (°)				-0.90†	0.27	9.7			
Vegetation features									
Lodgepole pine basal area				0.060	0.013	20.5			
Whitebark pine basal area				0.00092‡	0.00027	5.6			
Dead basal area (m ² /ha)				-0.35†	0.18	2.1			
Total ground cover (%)				-0.77†	0.21	11.0			
Current month's temperature (°C)	1.3†	0.64	2.9						
Age (adult)				0.71	0.23	6.9			
Time						5.5			
Julian date	5.7†	1.3	35.2	0.20	0.076				
Julian date ²				-0.00041	0.00017				
Statistics									
χ^2 (df) or F (num. df / den. df)	238	(1365)		193	(1379)		8.2	(1 / 24)	
P	1.000			1.000			0.009		
R_L^2 or R^2	0.89			0.90			0.25		

†Coefficient was estimated for values of the independent or dependent variables (x, y) transformed as $\ln([x, y] + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for this variable.

Mushrooms

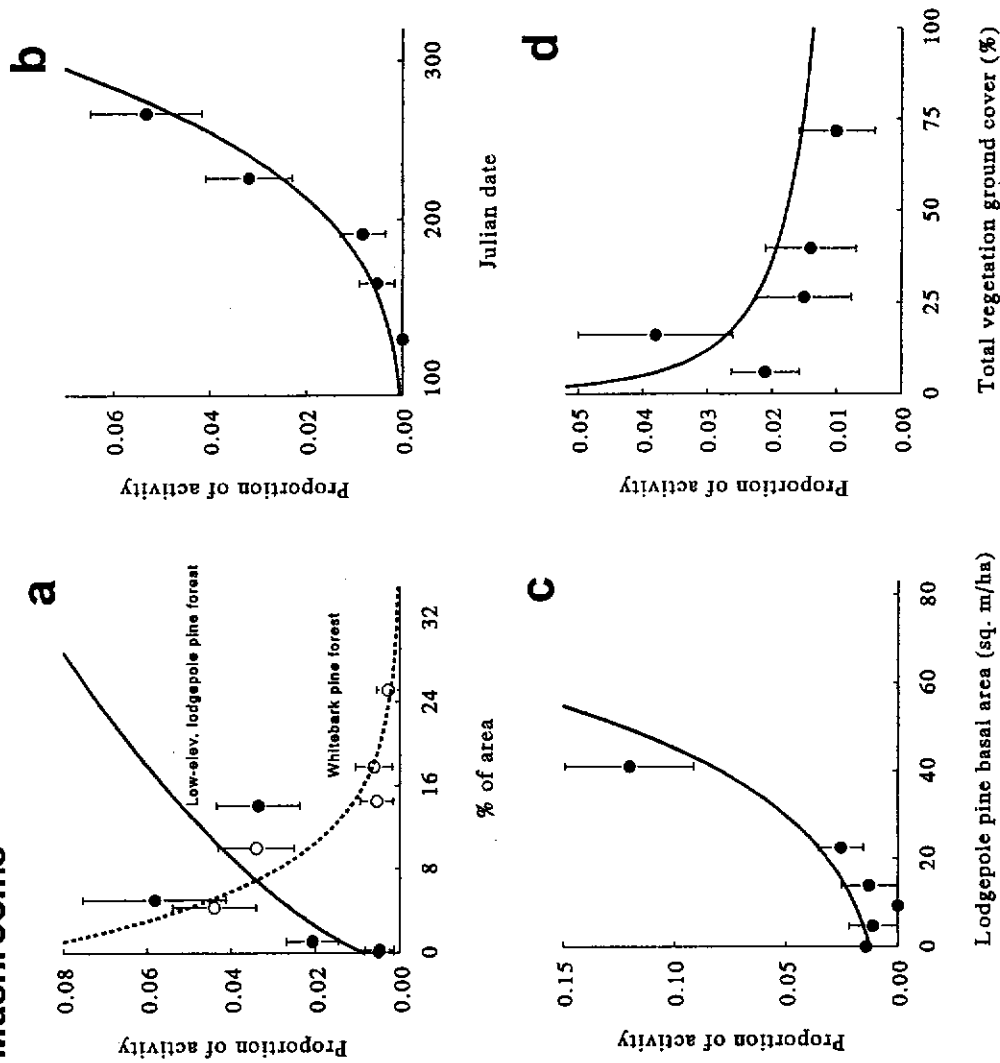


FIG. 24. Relations between grizzly bear use of mushrooms in the Yellowstone ecosystem, 1977-92, and variables denoting effects of (a) the extent of habitat types in the surrounding BMU, (b) date, (c) lodgepole pine basal area, and (d) total vegetation ground cover. Bear use is signified as the proportion of total activity involving excavation of mushrooms. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 29. Logistic regression models for the logit-transformed probability that a bear had been feeding on berries, related to variables pertaining to distal and proximal effects including food abundance, extent of habitat type, vegetation features, weather, type of bear, and time, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	-13	6.5		-390	116	
# of bison in ecosystem	-0.14†	0.57	4.0			
Extent of habitat type (% of BMU)						
High-elevation elk winter range	-0.62†	0.19	9.2			
Mesic Douglas-fir forest	0.77†	0.34	3.3			
Sheperdia abundance (index)				0.20‡	0.068	5.5
Shrub ground cover (%)				0.99†	0.26	16.4
Current month's temperature (°C)				-4.4†	1.9	3.8
Gender (female)	-0.42	0.21	2.1			
Time						
Julian date	3.6†	0.93	15.3	81†	24	25.9§
Julian date ²				-0.00084	0.00026	
Statistics						
χ^2 (df)	209	(1542)		135	(1144)	
P	1.000			1.000		
R_L^2	0.91			0.93		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for a given variable.

TABLE 30. Logistic regression models for the logit-transformed probability that sign of bedding was found at a telemetry location, related to variables pertaining to distal and proximal effects including food availability, extent of habitat types, site and vegetation features, weather, and type of bear, for grizzly bears in the Yellowstone ecosystem, 1977–92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	-3.1	1.4		-5.8	1.4	
Food availability in ecosystem						
# of whitebark pine cones (n /tree)	0.00039†	0.00016	4			
# of ungulate carcasses on transects	-0.38†	0.11	49	-0.28†	0.10	48
Extent of habitat or range types (% of BMU)						
High-elevation elk winter range	0.058	0.018	9			
Recently burned or harvested (dry)	-0.026	0.0099	5			
Mesic non-forest	-0.86†	0.33	5			
Mesic Douglas-fir forest				0.22†	0.12	11
Other feeding activities at site						47
Early-season use of ungulates				1.1	0.17	
Late-season use of ungulates				1.1	0.22	
Site features						
Elevation (m)				$1.5 \times 10^{-7}†$	7.3×10^{-8}	3
Slope (°)				0.055	0.018	13§
$\ln(\text{Slope} + 1)$				-0.81	0.20	
Total live basal area (m^2/ha)				0.020	0.0039	196
Weather						
Total winter ppt. (cm)	1.2†	0.35	11	1.7†	0.39	19
Cumulative growing season ppt. (cm)	-0.60	0.20	8			
Current month's ppt. (cm) ²	0.012	0.0036	8	0.034	0.013	11§
Current month's ppt. (cm)				-0.30	0.13	
Reproductive status (wt. COY)	-0.26	0.12	17	-0.24	0.14	3
Statistics						
χ^2 (df)	512	(539)		936	(1503)	
P	0.790			1.000		
R_L^2	0.52			0.56		

†Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§This Δ value includes the effects of removing both terms of the polynomial for a given variable.

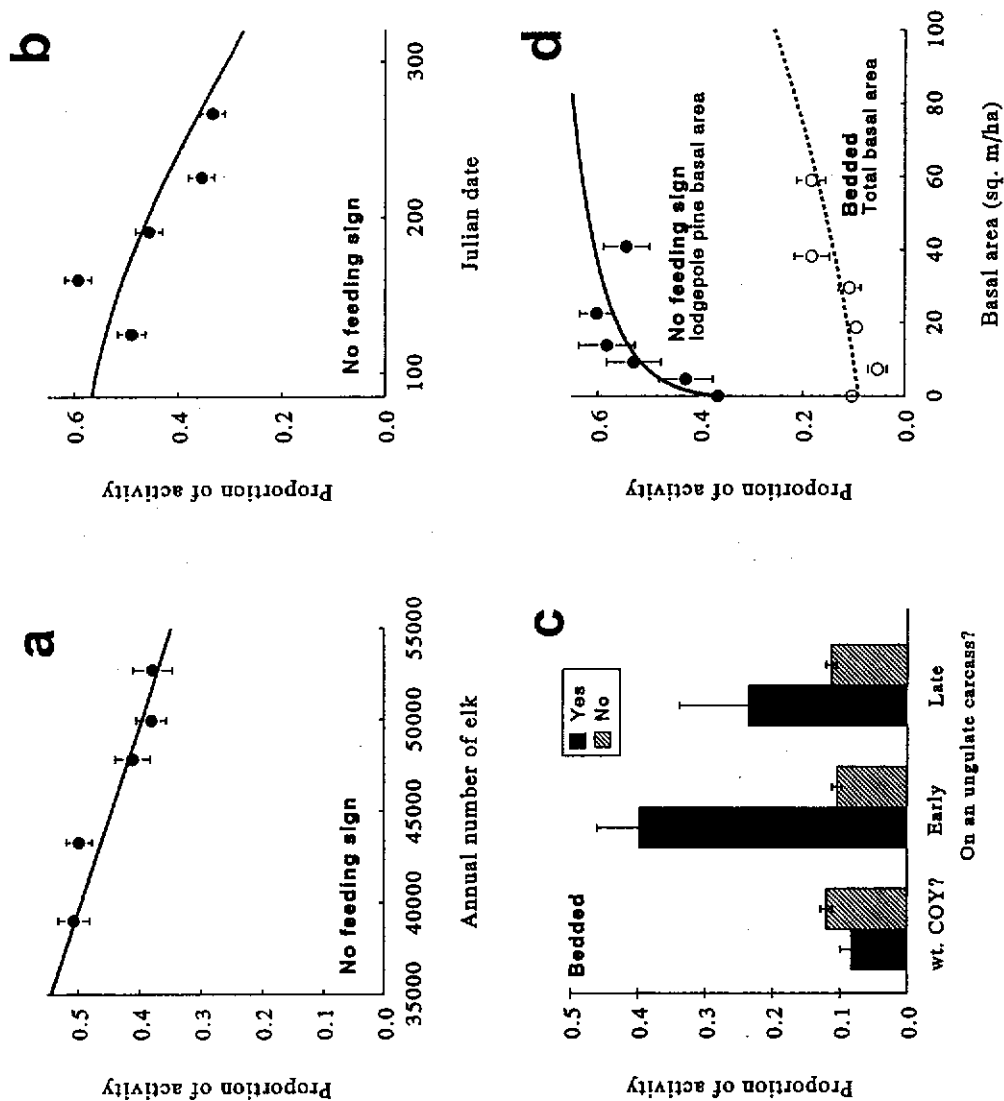


FIG. 25. Relations between bedding or the absence of feeding sign at a bear location in the Yellowstone ecosystem, 1977-92, and variables denoting (a) number of elk in ecosystem, (b) date, (c) reproductive status or co-occurrence of feeding on ungulates, and (d) forest basal area. Bear use is signified as the proportion of total activity with bedding or feeding sign absent. Points bracketed by standard error bars are proportions for quintiles or sextiles shown to illustrate goodness-of-fit.

likely when a bear was feeding on an ungulate carcass (Fig. 25c), where there was greater total forest basal area (Fig. 25d), or at higher elevations on intermediate slopes.

The likelihood that more than one bed was excavated at a bedding site depended on vegetation structure, the reproductive status of the bear, and the bear's activity. Several beds were more likely to be found where there was abundant coarse woody debris ($\Delta = 31.5$), where the bear was consuming an ungulate during Hyperphagia ($\Delta = 5.4$), or when the involved bear was a female accompanied by older young ($\Delta = 6.5$). The explicit model for the logit-transformed probability (p) of >1 bed is: $\text{logit}(p) = 0.11 + 0.94(\text{use of an ungulate}) + 0.022(\text{amount of coarse woody debris}^2) + 0.52(\text{wt. older young}) + 0.10(\text{wt. COY}) - 0.62(\text{without young})$; ($R^2_L = 0.18$, $\chi^2 = 24$, $df = 22$, $P = 0.343$).

No sign of feeding or bedding

The absence of feeding or bedding sign was interpreted as an instance where a marked bear was likely traveling when located by telemetry. This likelihood was less during years when elk populations were high (Fig. 25a) and bison populations low, and during years when ungulate carrion was abundant in Spring (Table 31). Sign of bedding or feeding was more common later in the growing season (Fig. 25b), during wet months or wet growing seasons, and following dry winters. Males less often left sign of feeding or bedding compared to females, especially during Hyperphagia. Proximally, sign of feeding or bedding was more often absent on sites with abundant lodgepole pine (Fig. 25d), or sparse graminoid or forb ground cover (Table 31). As expected from previous models, it was unlikely that feeding or bedding sign would be absent where yampa, biscuitroots, or clover were abundant. Sign of feeding and bedding also was less common at high elevations, on steep slopes, on sites with few live trees, and during years when whitebark pine cones were abundant.

Differences among bear classes in use of habitats

Females with COY compared to other classes

Sites used by females with COY were most distinguishable from adult males, year-round, and from subadult males during Hyperphagia. Such sites were least distinguishable from lone adult females during Spring and Estrus and from females with older young during Hyperphagia. Females with COY were more likely located in areas with extensive whitebark pine habitats, year-round, compared to all other bear classes except females with older young (Tables 32 & 33; Fig. 26). The nature of the relation of females with COY to whitebark

TABLE 31. Logistic regression models for the logit-transformed probability that no sign of feeding or bedding was found at a telemetry location, related to variables pertaining to distal and proximal effects including food availability, site and vegetation features, weather, type of bear, and time, for grizzly bears in the Yellowstone ecosystem, 1977-92. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable from the model.

Independent variable	Distal effects only			Proximal & distal effects		
	β_i	SE	Δ	β_i	SE	Δ
Constant	52.1	8.3		4.4	0.60	
Food availability in ecosystem						
# of whitebark pine cones (n/tree)				0.027	0.010	5
# of ungulate carcasses on transects	$-7.6 \times 10^{-6}\dagger$	1.8×10^{-6}	71	$-0.00001\dagger$	4.1×10^{-6}	27
# of bison	$1.5 \times 10^{-7}\dagger$	2.3×10^{-8}	45			
# of elk	$-5.1\dagger$	0.77	43	$-1.2 \times 10^{-9}\dagger$	1.9×10^{-10}	38
Food availability at site						
Abundance of biscuitroot (index)				$-1.7\dagger$	0.35	33
Abundance of yampa (index)				-0.52	0.099	31
Abundance of clover (index)				$-0.087\dagger$	0.035	5
Site features						
Elevation (m)				$-1.8 \times 10^{-7}\dagger$	5.8×10^{-8}	10
Slope ($^\circ$)				0.026	0.0067	15
Vegetation features						
Graminoid ground cover (%)				-0.012	0.0048	4
Forb ground cover (%)				$-0.00029\dagger$	0.00014	4
Lodgepole pine basal area (m^2/ha)				0.26\dagger	0.045	34
Total live basal area (m^2/ha)				$-0.00022\dagger$	0.000073	8
Weather						
Total winter ppt. (cm)	0.68\dagger	0.18	14			
Current month's ppt. (cm)	$-0.0046\dagger$	0.0023	17			
Cumulative growing season ppt. (cm)				$-0.0015\dagger$	0.00056	16
Gender (female)	-0.10	0.052	2			
Time						
Julian date	$-0.00002\dagger$	2.6×10^{-6}	52	$-0.00002\dagger$	3.6×10^{-6}	52
Post-1988 fires				-0.15	0.071	3
Statistics						
χ^2 (df)	923	(640)		1600	(1340)	
P	0.000			0.000		
R_L^2	0.06			0.15		

\dagger Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x+1)$.

\ddagger Coefficient was estimated for squared values of the independent variable.

TABLE 32. Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult female with cubs-of-the-year versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Spring and Estrus. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable.

Independent variable	vs. Adult males			vs. Subadult males			vs. Lone adult females			vs. Females wt. older young		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-4.3	0.86		146	75		-0.99	0.26		-2.7	1.1	
Distal factors — habitat types (% of BMU)												
Whitebark pine forest	0.086	0.024	11.6	0.0047†	0.0011	30.7	0.0023†	0.0008	8.6			
Rocky slopes & ridges	-0.68†	0.21	8.9							-0.070	0.28	4.4
Mesic non-forest				0.63†	0.35	1.3				1.4†	0.69	2.5
Mesic Douglas-fir forest				-0.81†	0.30	5.9						
Low-elevation elk winter range	0.10	0.025	14.7									
High-elevation elk winter range	-0.38†	0.12	7.9							-0.85†	0.28	9.2
Proximal factors — vegetation & site features												
Total forest basal area (m ² /ha)	-0.00035†	0.00016	6.8									
Live forest basal area (m ² /ha)							-0.022	0.0090	36.1			
Shrub ground cover (%)	0.25†	0.12	2.4							0.26†	0.11	4.1
On ungulate winter range										0.26	0.13	1.7
Elevation (m)	$5.1 \times 10^{-7}†$	1.4×10^{-7}	15.0	$1.8 \times 10^{-6}†$	0.8×10^{-6}	2.9§						
ln (elevation + 1)				-20	10							
Slope (°)							0.034	0.013	7.9	0.00073†	0.00032	5.9
Statistics												
χ^2 (df)	305	269		358	257		307	223		339	265	
P	0.065			0.000			0.000			0.001		
R_c^2	0.216			0.119			0.090			0.140		

†Coefficient was estimated for values of the independent variables (x) transformed as $\ln (x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

§The Δ includes effects of removing both terms of the polynomial for this variable.

TABLE 33. Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult female with cubs-of-the-year versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Hyperphagia. β_1 refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable.

Independent variable	vs. Adult males				vs. Subadult males				vs. Lone adult females				vs. Females wt. older young			
	β_1	SE	Δ		β_1	SE	Δ		β_1	SE	Δ		β_1	SE	Δ	
Constant	-1.9	1.1			-3.1	0.78			-3.3	0.79			0.80	0.42		
Distal factors — habitat types (% of BMU)																
Whitebark pine forest	0.84†	0.29	6.8		0.82†	0.32	4.8		0.66†	0.28	3.6					
Rocky slopes & ridges	-0.71†	0.22	9.4		-0.42†	0.19	3.1									
Mesic non-forest	-0.82†	0.42	1.8													
Mesic Douglas-fir forest									0.096	0.035	6.0		-0.038	0.021	1.4	
Low-elevation elk winter range	0.64†	0.18	12.7													
Proximal factors — vegetation & site features																
Yampa abundance (index)	0.24†	0.090	13.8		0.33†	0.12	10.6									
Shepherdia abundance (index)					-1.6†	0.64	5.2									
Globe huckleberry abundance (index)									-1.8†	0.62	9.2		-0.23†	0.098	6.5	
Total forest basal area (m ² /ha)	0.00023†	0.00010	9.6													
Live forest basal area (m ² /ha)					0.032	0.011	10.9									
Amount of woody debris (index)					0.39	0.11	11.8		0.89†	0.34	5.2		0.25	0.076	13.7	
Size of woody debris (index)					-0.41	0.13	13.7		-0.26	0.12	12.7					
Shrub ground cover (%)	-0.037	0.013	8.6													
Forb ground cover (%)					0.028	0.017	0.5									
Distance to forest edge (m)													-0.18†	0.074	13.5	
Slope (°)	0.074	0.017	19.0		0.0028†	0.0007	18.5									
Statistics																
χ^2 (df)	278	259			218	193			241	188			325	238		
P	0.195				0.000				0.005				0.001			
R_L^2	0.262				0.261				0.149				0.069			

†Coefficient was estimated for values of the independent variables (x) transformed as $\ln[(x) + 1]$.

‡Coefficient was estimated for squared values of the independent variable.

Females wt. COY vs. other classes

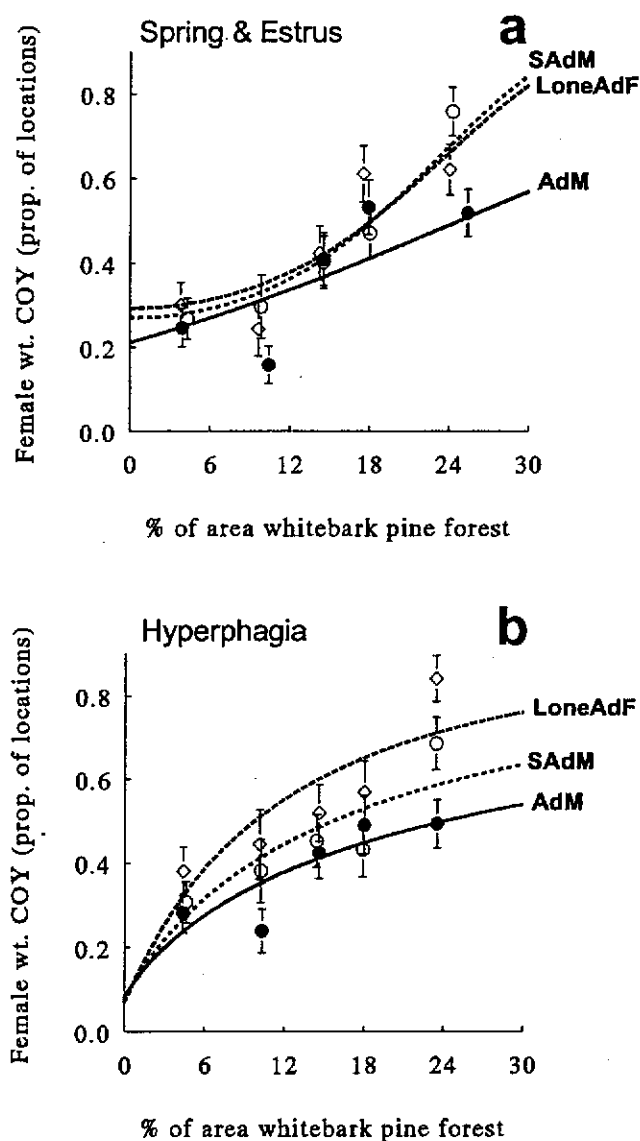


FIG. 26. Relations between the likelihood that a female with cubs-of-the-year (COY) had been located in the Yellowstone ecosystem, 1977-92, versus other classes of bears during Spring and Estrus and during Hyperphagia relative to the extent of whitebark pine forests in the surrounding BMU. Bear classes are: SAdM = subadult male; LoneAdF = lone adult female; and AdM = adult male. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

pine habitats relative to other bear classes changed between early and late seasons from convex to concave. This likely reflected the increased orientation of other bears to whitebark pine habitats during Hyperphagia as the motivation to eat increased and cone crops matured.

Otherwise, during Spring and Estrus, females with COY tended to be less common in areas with extensive high-elevation elk winter range compared to adult males and females with older young (Table 32). Females with COY also tended to use steeper slopes compared to other adult females. During Hyperphagia, females with COY used sites with greater amounts of coarse woody debris than any other class of bear except adult males (Table 33). The woody debris associated with female with COY locations also tended to be small, especially compared to that on sites used by lone adult females and subadult males. Also compared to subadult males, females with COY used sites with greater live forest basal area.

Adult males compared to other classes

Of all pairwise comparisons, sites used by subadult females and adult males year-round were the most distinguishable from each other (Tables 34 & 35). Otherwise, sites used by adult males were generally least distinguishable from sites used by subadult males or lone adult females and least distinguished of all from sites used by lone adult females during Spring and Estrus. Sites used by females with older young also were not clearly demarcated from sites used by adult males during Spring and Estrus.

Males of all ages were distinguished from females of all classes during Spring and Estrus by being located more often at lower elevations (Table 34; Fig. 27c). Additionally, adult males were less likely to be in areas with extensive low-elevation elk winter range or whitebark pine forests and more likely to be in areas with extensive rocky slopes and ridges compared to subadult males and all females except lone adults (Figs. 27a & 27b). Compared to subadult females, adult males also were more likely to use areas with extensive bison winter range. Compared to all females except those with COY, adult males were more likely to use sites with abundant lodgepole pine during Spring and Estrus. At the same time, adult males were less likely to use sites with large amounts of live forest basal area compared to subadult and lone adult females (Fig. 27d). Otherwise, compared to subadult females, adult males used sites with less forb cover and less standing dead basal area.

TABLE 34. Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult male versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Spring & Estrus. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable.

Independent variable	vs. Subadult males			vs. Lone adult females			vs. Females wt. older young			vs. Subadult females		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-1.1	0.89		2.9	0.67		2.6	0.57		3.1		1.4
Distal factors — habitat types (% of BMU)												
Whitebark pine forest	-0.36†	0.22	0.6				-0.072	0.017	15.8	-0.87†	0.36	4.1
Rocky slopes & ridges	0.92†	0.20	25.5				0.60†	0.16	13.8	0.90†	0.25	12.3
Mesic non-forest	1.4†	0.40	11.9				0.80†	0.31	4.8			
Mesic Douglas-fir forest										0.56†	0.26	2.7
Low-elevation elk winter range	-0.79†	0.17	25.6				-0.65†	0.13	24.8			
Bison winter range										0.17	0.042	16.3
Proximal factors — vegetation & site features												
Total forest basal area (m ² /ha)										0.84†	0.36	3.6
Live forest basal area (m ² /ha)				-0.25	0.084	7.3				-1.1†	0.30	14.8
Dead forest basal area (m ² /ha)										-0.77†	0.24	8.8
Lodgepole pine basal area (m ² /ha)				0.023	0.0096	3.8	0.24†	0.076	8.1	0.045	0.016	6.9
Shrub ground cover (%)	-0.29†	0.096	7.1									
Forb ground cover (%)										-0.042	0.016	8.0
On ungulate winter range							0.27	0.11	3.7	-0.47	0.21	3.1
Elevation (m)				-4.4×10 ⁻⁷ †	1.2×10 ⁻⁷	16.6	-2.9×10 ⁻⁷ †	1.1×10 ⁻⁷	7.3	-3.2×10 ⁻⁷ †	1.7×10 ⁻⁷	3.0
Statistics												
χ^2 (df)	211	163		385	293		456	361		222	241	
P	0.007			0.000			0.001			0.804		
R _c ²	0.095			0.068			0.130			0.377		

†Coefficient was estimated for values of the independent variables (x) transformed as $\ln [(x) + 1]$.

‡Coefficient was estimated for squared values of the independent variable.

TABLE 35. Logistic regression models of the relations of the logit-transformed probability that a location was that of an adult male versus other classes of bears, to distal and proximal factors, for grizzly bears in the Yellowstone ecosystem during Hyperphagia. β_i refers to an estimated parameter and Δ to change in AIC with deletion of the corresponding variable.

Independent variable	vs. Subadult males				vs. Lone adult females				vs. Females wt. older young				vs. Subadult females			
	β_i	SE	Δ		β_i	SE	Δ		β_i	SE	Δ		β_i	SE	Δ	
Constant	0.60	0.80			1.4	0.74			2.8	0.55			-3.5	2.7		
Distal factors — habitat types (% of BMU)																
Whitebark pine forest	0.73†	0.24	7.7		0.81†	0.22	15.8		-1.2†	0.48	4.6		1.7†	0.36	27.2	
Rocky slopes & ridges					0.15	0.047	10.3		5.4†	1.7	10.4					
Mesic non-forest																
Mesic Douglas-fir forest	-0.11	0.028	16.0						-0.13	0.030	20.9		-0.11	0.052	2.5	
Low-elevation elk winter range	-0.37†	0.10	11.5		-0.63†	0.18	12.8		-0.66†	0.15	20.7		-1.4†	0.36	18.1	
High-elevation elk winter range	0.043	0.015	6.3						0.38†	0.13	6.3		1.1†	0.48	3.4	
Bison winter range									-0.57†	0.18	9.1		0.22	0.051	19.3	
Proximal factors — vegetation & site features																
Yampa abundance (index)					-0.27†	0.080	19.0		-0.83	0.24	33.1					
Biscuitroot abundance (index)	1.3†	0.71	2.0													
Globe huckleberry abundance (index)	0.94†	0.46	2.7													
Live forest basal area (m ² /ha)									-0.023	0.0082	21.0		-0.30†	0.12	9.0	
Lodgepole pine basal area (m ² /ha)	0.25†	0.089	5.8													
Shrub ground cover (%)									0.041	0.012	12.6		0.029	0.029	2.7	
Forb ground cover (%)									0.32†	0.14	9.2					
Graminoid ground cover (%)													-0.034	0.012	25.7	
Elevation (m)	-2.5×10 ⁻⁷ †	1.2×10 ⁻⁷	3.8		-2.5×10 ⁻⁷ †	1.1×10 ⁻⁷	3.9									
Slope (°)					-0.0011†	0.0005	2.6		-0.057	0.017	10.7		-0.083	0.020	18.6	
Statistics																
χ^2 (df)	367	285			370	300			319	290			208	241		
P	0.001				0.004				0.116				0.941			
R ²	0.137				0.174				0.251				0.419			

†Coefficient was estimated for values of the independent variables (x) transformed as $\ln(x + 1)$.

‡Coefficient was estimated for squared values of the independent variable.

Adult males vs. other classes (Spring & Estrus)

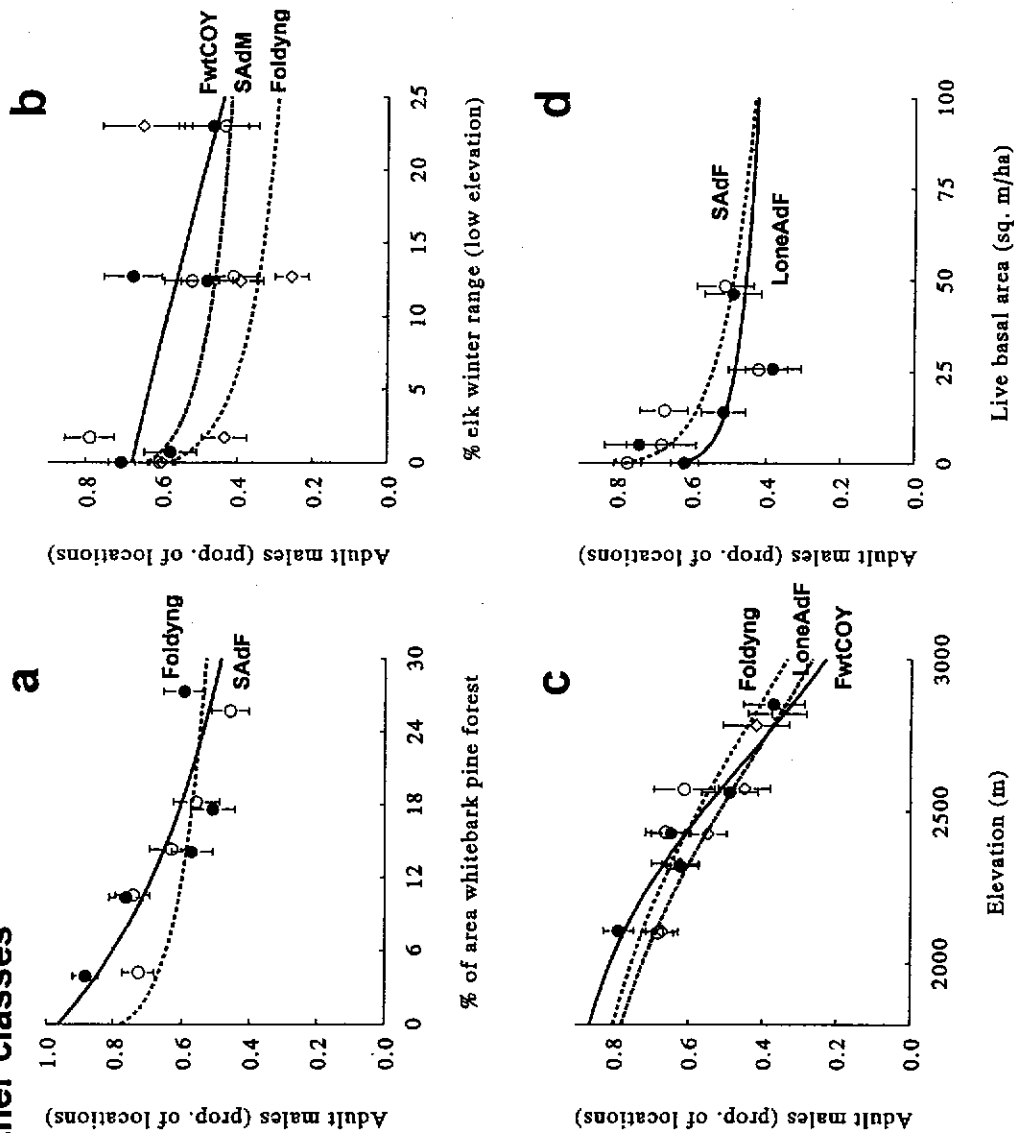


FIG. 27. Relations between the likelihood that an adult male had been located in the Yellowstone ecosystem, 1977-92, versus other classes of bears during Spring and Estrus relative to the extent of habitat types in the surrounding BMU, elevation, and forest basal area. Bear classes are Foldyng = females with older young; SAdF = subadult female; FwrcOY = female with COY; SAdM = subadult male; LoneAdF = lone adult female. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

During Hyperphagia, adult males were less likely than any other class of bear to be in areas with extensive low-elevation elk winter range (Table 35). Conversely, adult males were more likely to be in areas with extensive high-elevation elk winter range and few mesic Douglas-fir habitats compared to subadults of both genders and females with older young (Fig. 28a). Adult males were similarly more likely to be in areas with extensive rocky slopes and ridges or mesic non-forest habitats compared to all females except those with older young. Proximally, males of all ages were more likely to be on gentle slopes than females of any class (Tables 33 & 35; Fig. 28b). Adult males also were less likely to use sites with abundant yampa or extensive shrub cover compared to adult females or females accompanied by young, respectively (Figs. 28c & 28d). Compared to females with older young and subadult females, adult males were more likely to use sites with extensive forb cover and less likely to use sites with extensive graminoid cover, respectively. Among males, subadults were more likely than adults to use sites with considerable lodgepole pine basal area.

Activities of individual males and females

Based on records of activity for individual bears, females excavated whitebark pine seeds and roots more often than did males (MANOVA, Wilks' $\Lambda = 0.82$, $df = 2/78$, $P = 0.0005$; Table 36). Use of roots by bears was substantially correlated with their use of proteinaceous foods, lack of feeding sign, use of berries, use of late-season rodents, and use of fibrous grazed foods. Standardized canonical coefficients of each activity for the canonical correlation with root use were -0.29 , -0.41 , 0.35 , 0.53 , and 0.57 , respectively. Canonical $R = 0.52$ ($F = 5.6$, $df = 5 / 75$, $P = 0.0002$). By implication, root use potentially indicated foraging strategies that affected a number of activities. Use of whitebark pine seeds was not substantially correlated with any other activity. The proportions of locations where bears used roots, Hymenoptera, or high-quality vegetal foods, or where no feeding sign was found were the most variable among bears of any types of activity (Table 36). Use of berries, fatty foods, late-season rodents, and proteinaceous foods were least variable.

Range size and movements

With the exception of 50% ranges, movements and range sizes of males showed little or no relation to potential explanatory variables. Estimated 50 and 95% range sizes for males and females, respectively, were sensitive to the number of relocations used, even at $n > 30$ (Tables 37). Distances between successive locations were not. Females that had been

Adult males vs. other classes (Hyperphagia)

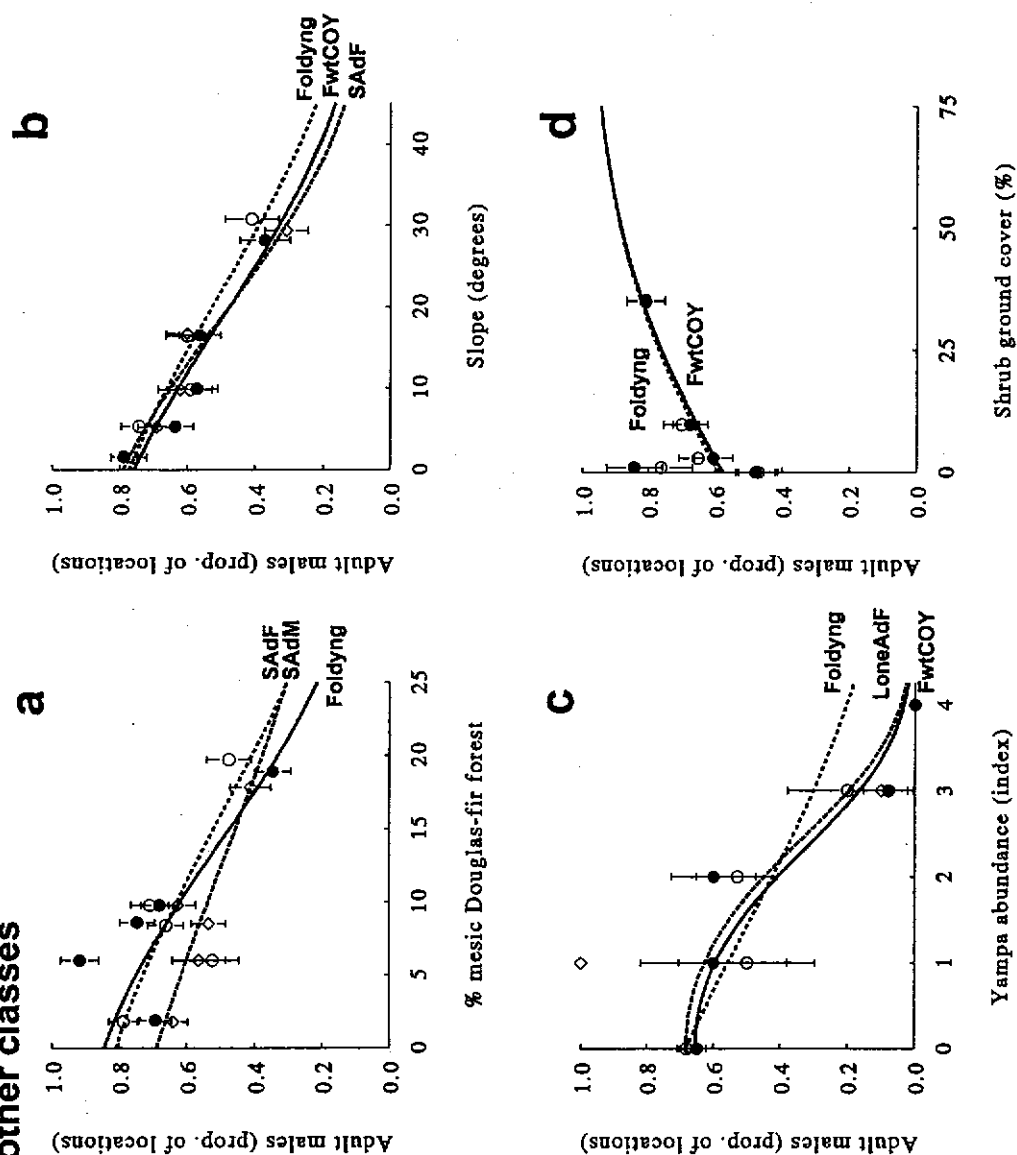


FIG. 28. Relations between the likelihood that an adult male had been located in the Yellowstone ecosystem, 1977-92, versus other classes of bears during Hyperphagia relative to the extent of habitat types in the surrounding BMU, slope, yampa abundance, and the extent of shrub cover. Bear classes are SAdF = subadult female; SAdM = subadult male; Foldyng = females with older young; FwtCOY = female with COY; & LoneAdF = lone adult female. Points bracketed by standard error bars are proportions for quintiles shown to illustrate goodness-of-fit.

TABLE 36. The proportion of activities at radiotelemetry locations and variation in those proportions among individuals, by gender, for individual Yellowstone grizzly bears, 1977–92. Mean proportions were estimated weighted by number of observations of activity per individual bear. Variation is expressed as coefficient of variation ($CV = \bar{x}/SD$) calculated on natural log transformed proportions ($\ln[1 + p]$).

Type of activity	Females		Males	
	\bar{x}	CV	\bar{x}	CV
Use of high-protein food	0.028	1.98	0.033	1.71
Use of whitebark pine seeds	0.092	2.99	0.057	2.19
Use of high-fat foods	0.018	1.40	0.018	1.34
Use of roots	0.112	3.45	0.051	2.04
Use of Hymenoptera	0.131	3.25	0.112	2.78
Use of high-quality vegetal foods	0.139	3.78	0.121	3.01
Use of fibrous foods	0.031	2.06	0.035	1.74
Use of rodents Hyperphagia	0.017	1.58	0.013	1.05
Use of berries	0.017	1.56	0.021	1.47
Bedded	0.076	2.88	0.080	2.55
No sign of feeding or bedding	0.341	4.83	0.355	4.09
<i>n</i>	46		35	

TABLE 37. Regression models for the relations of movements and multi-annual range sizes (50% and 95%) to effect of management translocation, number of telemetry locations, body size, % of locations by reproductive status, % of locations by season, and activity of grizzly bears in the Yellowstone ecosystem, 1977-92. Observations were weighted by the sample size of activity for each bear.

Independent variable	Females						Males					
	Mean distance between successive locations (ln[n + 1])			Adaptive kernel 50% range (ln[km ² + 1])			Adaptive kernel 95% range (ln[km ² + 1])			Adaptive kernel 50% range (ln[km ² + 1])		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	8.0	0.23		6.2	0.79		13.5	1.4		9.1	0.76	
Management translocation							0.84	0.21	3.83			
Number of relocations (ln[n + 1])							0.39	0.14	1.01	0.55	0.19	0.78
Body size												
Lean body volume (index)										-0.0024	0.00071	2.03
Lean body volume deviance (index)										0.0048	0.0012	3.66
Reproductive status†												
Locations while alone	-0.056	0.014	3.73	-0.25	0.052	6.41						
Locations with COY	-0.070	0.016	4.87									
Locations with young >1 yr	-0.058	0.016	3.18	-0.16	0.054	11.9						
Season†												
Locations during Hyperphagia	0.29	0.058	6.69	0.92	0.20	5.56						
Locations during Estrus							-1.3	0.34	3.68			
Activity‡												
Use of fibrous grazed foods				-0.33	0.097	2.42				-0.30	0.11	0.16
Use of roots												
Statistics												
F (df num. / df den.)	14.3	(4 / 41)		10.9	(4 / 41)		15.7	(3 / 41)		6.0	(4 / 26)	
P	0.000			0.000			0.000			0.002		
R ²	0.58			0.52			0.53			0.48		

†Expressed as % of total relocations, by individual bear, transformed as ln(% + 1).

‡Expressed as % of total activity, by individual bear, transformed as ln(% + 1).

translocated by managers had 95% ranges larger than those of other bears of the same gender. Such an effect was not evident for males. By implication, pre-analysis efforts to censor the effects of management transports were adequate for males, but not for females. Females also tended to move less and maintain smaller 50% ranges while alone or accompanied by older young. Females and males exhibited smaller 50% ranges while using fibrous grazed foods and roots, respectively.

Movements of males and females were differentiated by within-gender effects of season and lean body volume (*LBM*). There were no effects of season on males. However, females tended to have larger 50% ranges and more extensive movements during Hyperphagia, and smaller 95% ranges during Estrus (Fig. 29a). Conversely, there was no effect of lean body volume on females, whereas males that were younger or large for their age had larger 50% ranges (Tables 37; Fig. 29b). These differences were in addition to the larger ranges and longer movements previously documented for males compared to females (Blanchard & Knight, 1991).

Corpulence and relative lean body volume

Indices of corpulence calculated for bears from Kluane National Park, Yukon, Canada, were moderately correlated with % body fat estimated by electrical bioimpedence analysis; $r = 0.66$ for corpulence based on scale weights (CRP_{sw}) and $r = 0.58$ for corpulence based on body volume (CRP_{bv}). Percent body fat (*FAT*) can be estimated from CRP_{sw} for this population as: $FAT = 18.6 + 7.7CRP_{sw}$ ($r^2 = 0.44$, $df = 1/65$, $F = 51.5$, $P < 0.001$). Body fat can be estimated from CRP_{bv} as: $FAT = 19.9 + 6.9CRP_{bv}$ ($r^2 = 0.34$, $df = 1/65$, $F = 33.2$, $P < 0.001$).

Male and females exhibited relations between gross morphology and factors such as age, reproductive status, movements, and date (Tables 38 & 39). Among females, terminal measures of corpulence (by scale weight) were negatively associated with the extent of movements. Corpulence (by scale weight) of females and lean body volume of males were positively associated with Julian date (Fig. 30a). In other words females tended to become more corpulent during the course of the active season whereas males tended to gain lean body volume. Subadult males tended to be less corpulent (by body volume) than adult males, whereas females tended to be more corpulent (by body volume) compared to others of their gender when accompanied by COY.

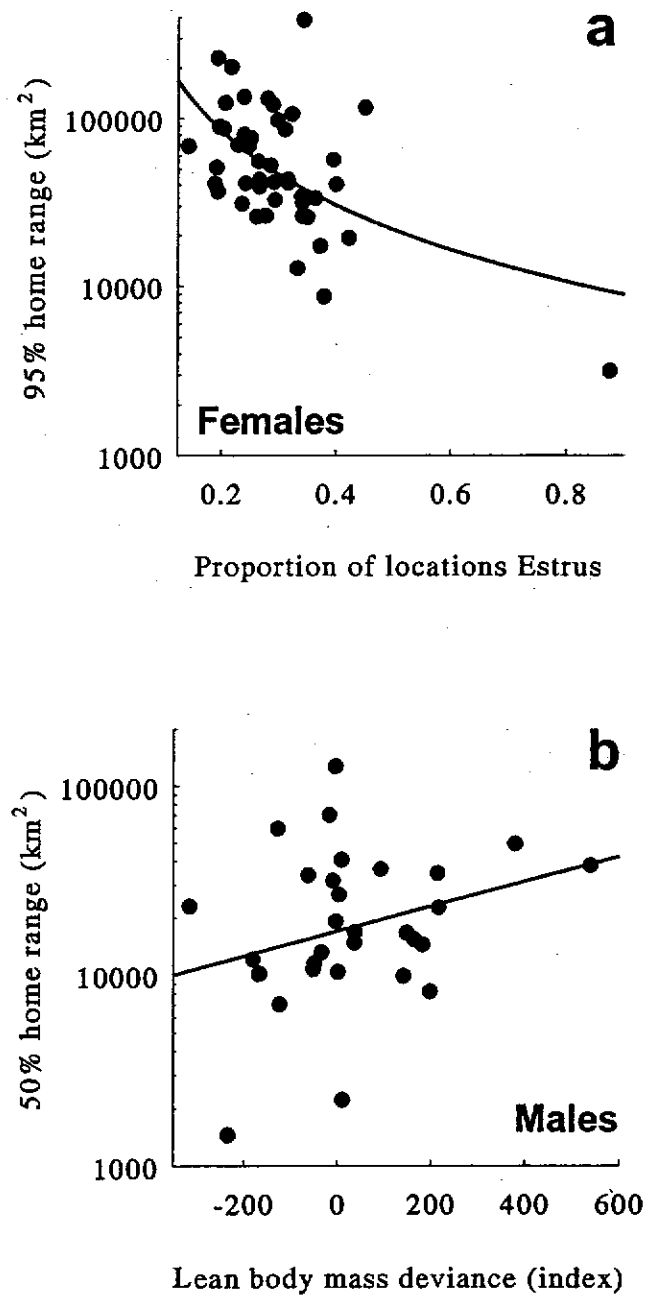


FIG. 29. Relations between (a) 95% home range size and proportion of locations obtained from females during Estrus and (b) 50% home range size and relative lean body mass of males, for Yellowstone grizzly bears, 1977-92.

TABLE 38. Regression models for relations of body morphology to movements, date, % of relocations by reproductive status, and activity of female grizzly bears in the Yellowstone ecosystem, 1977-92. Models are presented for individual bears regardless of when they were weighed or measured relative to the period during which observations of activity were made (all measures), and only including weights and measurements at either the mid-point or end of the observation period (terminal measures). Observations were weighted by the sample size of activity for each bear.

Independent variable	Lean body mass deviance (index residuals)						Corpulence by body volume (residual dm ³)						Corpulence by scale weight (residual dm ³)					
	All measures			Terminal measures			All measures			All measures			All measures			All measures		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	72	50		496	120		0.050	0.47		-2.2	6.7		-34	3.7				
Distance between successive locations†										-1.8	0.73	0.05						
Julian date‡										3.3	0.67	5.45	4.9	0.55	9.42			
Locations with COY‡							0.30	0.13	0.00									
Activity§																		
Use of roots	-52	21	0.33	-152	32	4.56												
Bedded				-116	35	1.60	0.25	0.094	0.79									
Use of rodents (hyperphagia)													0.51	0.15	0.91			
No feeding sign													2.2	0.49	2.82			
Statistics																		
F (df num. / df den.)	6.0	(1/40)		11.8	(2/17)		5.5	(2/38)		13.0	(2/24)		30.4	(3/10)				
P	0.019			0.001			0.008			0.000			0.000					
R ²	0.13			0.58			0.22			0.52			0.90					

†Coefficients calculated for independent (x) variable transformed as $\ln(x + 1)$.

‡Expressed as % of total relocations, by individual bear, transformed as $\ln(\% + 1)$.

§Expressed as % of total activity, by individual bear, transformed $\ln(\% + 1)$.

TABLE 39. Regression models for relations of body morphology to date, % of relocations obtained as a subadult, and activity of male grizzly bears in the Yellowstone ecosystem, 1977-92. Models are presented for individual bears regardless of when they were weighed or measured relative to the period during which observations of activity were made (all measures), and only including weights and measurements at either the mid-point or end of the observation period (terminal measures). Observations were weighted by the sample size of activity for each bear.

Independent variable	Lean body mass deviance (index residuals)						Corpulence by body volume (residual dm ³)					
	All measures			Terminal measures			All measures			Terminal measures		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-1643	593		-92	50		0.45	0.44		1.4	0.46	
Julian date†	318	113	0.96									
Locations as a subadult‡							-0.26	0.086	1.21	-0.311	0.11	0.10
Activity§												
Use of roots				79	30	0.19	-0.49	0.15	1.71	-0.57	0.19	0.43
Bedded							0.39	0.15	0.31			
Statistics												
F (df num. / df den.)	7.9	(1/29)		7.1	(1/13)		8.0	(3/27)		6.8	(2/12)	
P	0.009				0.019			0.001		0.011		
R ²	0.21				0.35			0.47		0.53		

†Coefficients were estimated using independent variables (x) transformed as $\ln(x + 1)$.

‡Expressed as % of total locations, by individual bear, transformed as $\ln(\% + 1)$.

§Expressed as % of total activity, by individual bear, transformed as $\ln(\% + 1)$.

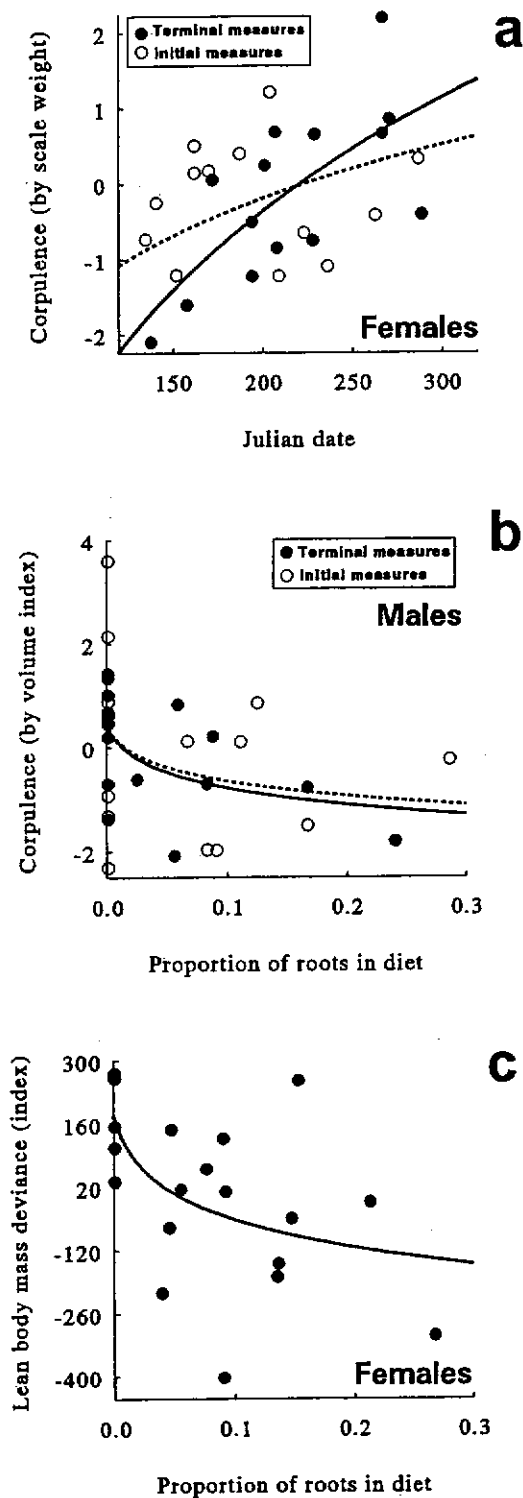


FIG: 30. Relations between (a) Julian date and corpulence of females (as indexed by scale weight), and between the consumption of roots and (b) corpulence of males (as indexed by body volume) and (c) relative lean body mass of females, for Yellowstone grizzly bears, 1977-92.

Among both genders, gross morphology was consistently associated with frequency of bedding or use of roots (Table 39). Females that more often used roots tended to be small for their age (Fig. 30c), whereas males that more often ate roots tended to be large but thin (Fig. 30b). Corpulent males and females tended to bed more often, whereas females that were large for their age tended to bed infrequently. Otherwise, corpulent (by scale weight) females more often excavated rodents during Hyperphagia or left no sign compared to thin females.

Female reproduction

Using individual marked females as units of analysis, an estimated 0.81 and 0.79 cubs were produced per year (yr) using animals with ≥ 1 and ≥ 3 yrs of observation, respectively (Table 40). Assuming a 3-yr reproductive interval, this equated to litters averaging about 2.4 cubs. No other effects were evident for cub production. By contrast, cub losses were related to female age and activities. Older females tended to lose more cubs. In addition, females that used proteinaceous foods more often tended to lose more cubs, whereas females that used ants and hornets more often tended to lose fewer cubs. Use of fatty foods also was associated with a tendency to lose cubs.

Using annual observations of females as units of analysis, female age affected annual probability of producing a litter, probability that only a singleton would be produced, and the probability that at least one cub would subsequently be lost (Table 41). The likelihood that a female would produce a litter was complexly related to her age, rapidly escalating after the age of 3, reaching a maximum at about the age of 10, declining to a secondary minimum at about the age of 17, and escalating thereafter (Fig. 31). The 2 age-related peaks in likelihood of litter production mirrored the effects of age on likelihood of cub loss (Table 41); i.e., after the advent of sexual maturity, elevated cub loss resulted in the more frequent production of litters compared to females at their most competent, roughly between the ages of 13 and 20. Senescence also was evident in increased likelihood that only a singleton would be produced (Fig. 32a). There was no other effect on this likelihood (Table 41).

Use of whitebark pine seeds had a strong effect on the likelihood that a female would produce 3 cubs and a lesser, positive, effect on the likelihood that she would produce a litter of any size (Table 41; Fig. 31). Females that were captured in areas where, on average, they ate more pine seeds or during and following years when more pine seeds were available were

TABLE 40. Regression models for the relations of number of cubs observed and number of cubs subsequently lost, by individual bear, to duration of observations per bear, median maternal age, and maternal activity, for female grizzly bears in the Yellowstone ecosystem, 1977-92. Models are presented for individual bears with ≥ 1 and ≥ 3 yrs of observations.

Independent variable	Number of cubs observed						Number of cubs lost					
	≥ 1 yrs of observations			≥ 3 yrs of observations			≥ 1 yrs of observations			≥ 3 yrs of observations		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-0.30	0.39		-0.20	1.1		0.83	0.31		0.45	0.32	
Years of observations (n)	0.81	0.11	17.3	0.79	0.23	2.1						
Median female age (yrs ²)										0.0035	0.00099	1.98
Activity†												
Use of high-protein foods							0.29	0.12	0.12	0.35	0.11	1.02
Use of Hymenoptera							-0.29	0.12	0.21	-0.37	0.10	2.34
Use of high-fat foods										0.31	0.10	0.75
Statistics												
F (df num. / df den.)	55.4	(1 / 44)		11.9	(1 / 21)		5.6	(2 / 29)		8.9	(4 / 17)	
P	0.000			0.002			0.009			0.000		
R^2	0.56			0.36			0.28			0.68		

†Expressed as % of total activity, by individual bear, transformed as $\ln(\% + 1)$.

TABLE 41. Logistic regression models of the annual probability of producing a litter, and given a litter, the probability that the litter consisted of 1 or 3 cubs and that at least one cub was lost to natural causes, related to maternal age, food availability, and maternal activity, for female grizzly bears in the Yellowstone ecosystem, 1977-92.

Independent variable	Annual probability of producing a litter			Probability of litter size =					
				1 cub			3 cubs		
	β_i	SE	Δ	β_i	SE	Δ	β_i	SE	Δ
Constant	-18	4.8		-2.7	0.55		11	4.9	
Type of bear									
Female age (yrs)	-1.6	0.50	12.1				-0.94	0.41	4.03
Female age (yrs ²)							0.038	0.016	5.83
Female age (yrs ³)	0.00094	0.00034	6.61	0.00027	0.00011	44.1			
Female age (ln[yrs + 1])	13	4.0	18.0						
Food availability									
Whitebark pine cone crop, previous yr (n/tree)	0.33§	0.17	8.65				0.0015†	0.00055	6.86
Whitebark pine cone crop, current yr (n/tree)							0.0014†	0.00054	5.29
Activity†									
Use of whitebark pine seeds							0.021†	0.0088	4.32
Use of roots							-1.2§	0.61	1.57
Use of high-protein foods									
Use of rodents (Hyperphagia)							2.6§	0.99	5.37
Use of quality vegetal foods							4.8†	2.0	3.58
Statistics (goodness-of-fit)							-4.8§	2.0	4.22
χ^2 (df)	154	(154)		12.5	(16)				
P	0.480			0.710					
R ²	0.31			0.56					
							41.5	(46)	
							0.661		
							0.42		

†Expressed as % of total activity, by Bear Management Unit (BMU).

‡Coefficient was estimated for squared values of the independent variable.

§Coefficient was estimated for values of the independent variable (x) transformed as $\ln(x + 1)$.

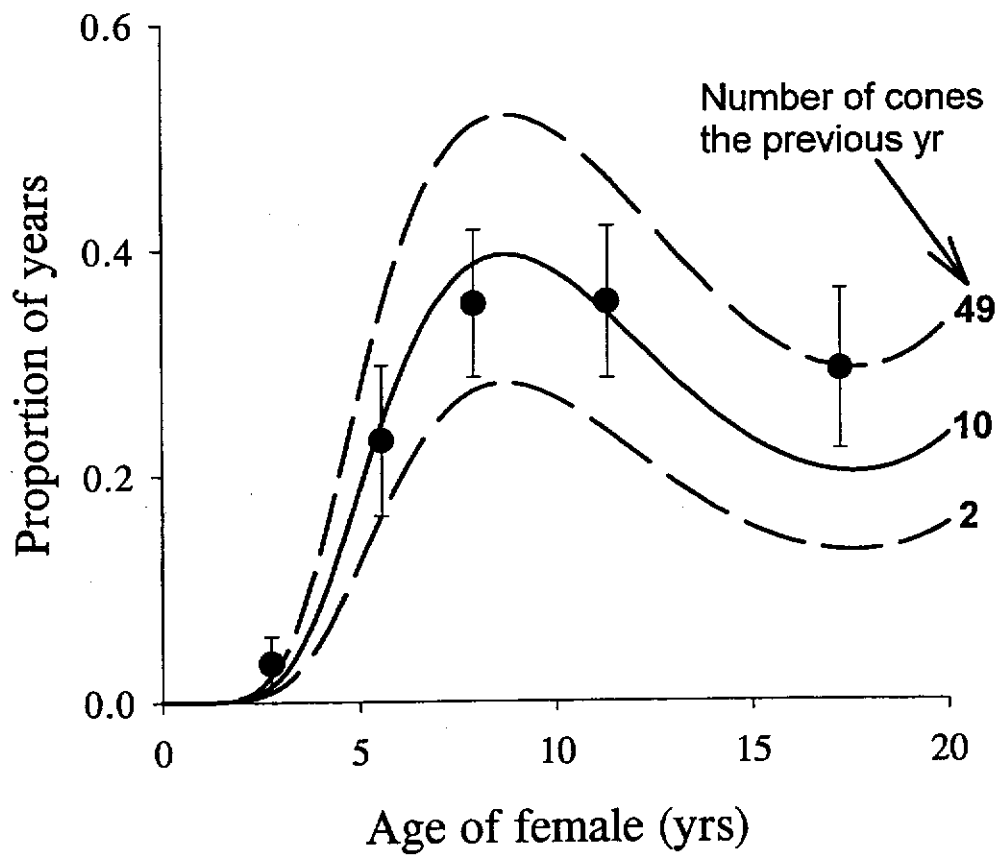


FIG. 31. Relation between the proportion of years that a female was observed with cubs and her age. Relations are shown for years following large (45), average (10), and small (2) whitebark pine cone crops expressed as average number of cones per tree at permanent transects.

Litter size

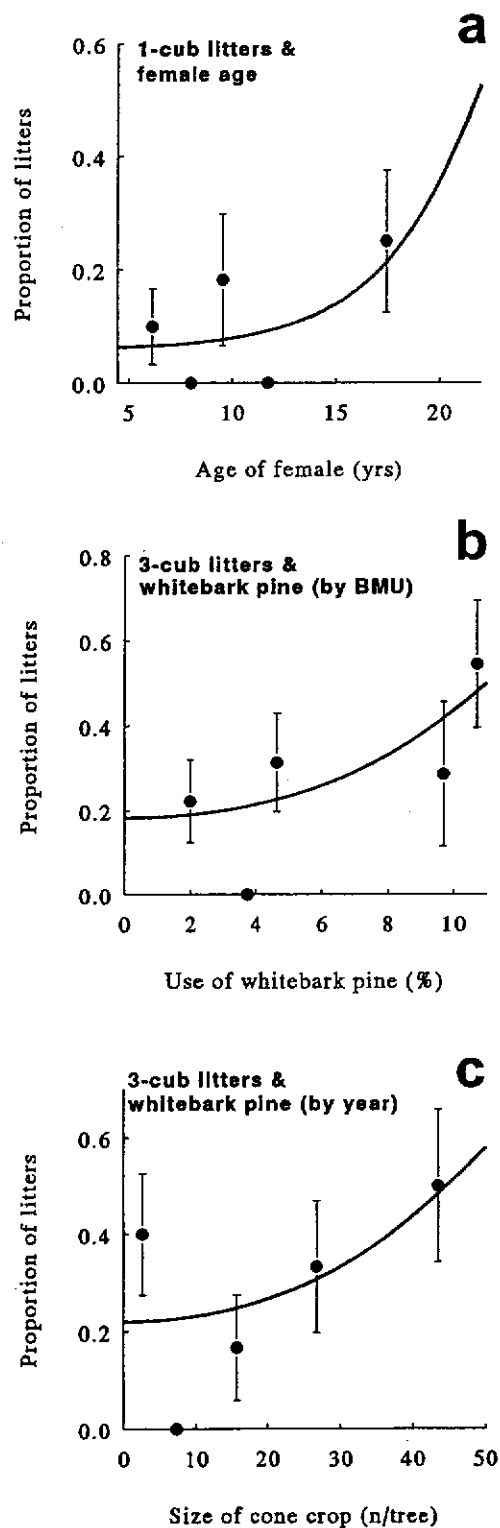


FIG. 32. Relations between proportions of litters with 1 (a) or 3 (b & c) cubs observed with female grizzly bears in the Yellowstone ecosystem, 1977-92, and age of the dam, extent of whitebark pine forests in the surrounding BMU, or size of the whitebark pine cone crop the previous year. Points bracketed by standard error bars are proportions of quintiles shown to illustrate goodness-of-fit.

more likely to produce 3-cub litters (Figs. 32b & 32c). By contrast, females captured in areas where, on average, they ate more roots produced relatively fewer 3-cub litters. In common with the results using individual females as units of analysis, females that more often ate proteinaceous foods lost more cubs compared to females that ate more of other foods. The same pattern held true for females that more often used rodents or rodent food caches during Hyperphagia. By contrast, cubs of females that ate more high-quality vegetal foods more often survived.

Correlations among activities

Many activities were spatially and temporally associated. As a consequence, each carried information about other activities when entered as an independent variable in the preceding models. Such was the case for grizzly bear use of roots described earlier. These types of correlations also are germane when variables denote infrequent or low-quality feeding activities. Of the following: bedded, no sign of bedding or feeding, use of fibrous foods, use of quality vegetal foods, and use of rodents during Hyperphagia; only the last two activities exhibited strong correlations among individuals with the occurrence of other activities. Among females, late-season use of rodents was positively correlated with bedding and use of roots (Canonical $R^2 = 0.26$, $F = 7.55$, $df = 2 / 42$, $P = 0.002$). Standardized canonical coefficients for each were 0.62 and 0.92, respectively. Also among females, use of quality vegetal foods was positively correlated with use of Hymenoptera ($r^2 = 0.16$, $F = 8.23$, $df = 1 / 44$, $P = 0.006$).

Discussion

Biases and bias control

None of this study's sampling was randomized. At best, trapping effort was representative of areas within the Yellowstone region. Changes in study priorities and logistical and political constraints strongly affected the timing, distribution, and intensity of effort. Adult males very likely were captured and marked disproportionately more often than other bear classes (Pease & Mattson, 1999), presumably because their large ranges made them more vulnerable to capture. Location of marked bears by aerial telemetry tended to be systematic with respect to days, but diurnally was heavily biased towards early daylight hours (Unpublished analysis). As with trapping effort, visitation of telemetry locations by field crews was constrained by lack of access to the mostly-roadless study area. I deployed the limited number of personnel to maximize information return. I strove to be representative of marked bears, but also modified the effort to sample representatively across the study area and among different bear classes. Temporally, Spring was under-sampled compared to other seasons because of fewer field crews and more difficult field conditions during this time of year.

Randomized assignment of treatments to experimental units is used in experimental design to control for extraneous effects (Wold 1956; Fisher, 1960). Under field conditions, sampling can be randomized with respect to some factor(s), but often as a poor substitute for the randomized assignment of treatments (Fisher, 1960; Cochran, 1983). In all instances, the issue is control of effects extraneous to those that are the focus of a given study. Under field conditions this becomes especially problematic, even with randomized sampling, because of the many factors potentially affecting measured responses at different scales (Green, 1979; Cochran, 1983). In fact, without attention to complexities of the sampled organisms and their environment, randomized sampling can lead to a dangerous sense of complacency.

Modeling offers an alternate means of controlling for the effects of many factors under field conditions (Wold 1956; Green 1979; Cochran, 1983; Hilborn & Mangel, 1997; Burnham & Anderson, 1998). It can be used alone, or in conjunction either with randomized sampling or randomized assignment of treatments. When used alone, reliable statements about the effects of single factors require that special conditions be met. In particular, the suite of factors considered for inclusion in a model must be biologically plausible and

sufficiently replete to cover the major effects likely operational during the study. Failure to anticipate and estimate some major effect compromises use of a model for inferences because all of the effects that were estimated potentially remain affected by substantial unknown bias. There are no unequivocal standards by which models can be judged in this regard, other than biological plausibility and goodness-of-fit (Hilborn & Mangel 1997). Thus, models with the most merit are those that fit the data well (e.g., have an R^2 approaching 1) and contain effects of a nature and type consistent with biological knowledge. Consistency with models fitted to other data or derived by other analytical approaches also serves as confirmation. As discussed in the methods, I used modeling to control what would otherwise be bias. Model selection based on information-theoretic criteria helped balance reduction of bias and specification of uninformative or "spurious" effects (i.e., "over-fitting"; Burnham & Anderson, 1998). The former is the benefit and the latter is the risk of including more variables in a model.

This approach can be illustrated by an example. Without any inferential structure provided by sampling design and/or a model, the activity of a marked bear at a given telemetry location has essentially no known relation to the population. However, in this usage, the 'population' includes bears of all ages, genders, and reproductive status, at all places in time and space. However, the information imparted by this theoretical single location would increase dramatically if it was attributable to the 'population' of locations for adult males, during Spring, on Julian date 100, in a BMU covered by 25% high-elevation elk winter range, following a winter when 30 cm of ppt fell, during a month when an additional 10 cm of rain fell, at a site with abundant pre-flower bluegrass. As more and more effects are specified, the outcome at that location becomes more certain. Put another way, more effects equate to more 'populations' or 'reference classes.' As was noted in the methods, this process "...is often simply the problem of finding the appropriate reference class, that is, the class [to] which a certain subject is, relative to our body of knowledge, a random member" (Kyburg 1969). Practically speaking, residual variation contains remaining bias, and when residuals become small enough, the potential effects of bias become inconsequential (Rosenbaum 1984). In other words, at little risk, the observation can be treated as random, at least with respect to the class to which it is assigned. In a modeled field setting, a class is the

approximate analog of a treatment in a controlled experiment. Again, the validity of this approach is contingent on biological plausibility.

The potential effect of diurnal bias in telemetry locations was not addressed in the modeling process because I did not include time-of-day in any model. However, I concluded that this bias probably was not substantial for several reasons. For one, the roughly 400-m diameter within which observed activity was ascribed to a location encompassed much of what grizzly bears in Yellowstone typically use during a 24 hour period (Schleyer *et al.*, 1984; Haroldson & Mattson, 1985). For another, the proportion of activity occurring in non-forest areas, round the clock (Schleyer *et al.*, 1984; Haroldson & Mattson, 1985), was roughly the same as what one would detect given the diurnal distribution of aerial locations obtained during this study (Unpublished analysis). Although diurnal bias should not be trivialized, these considerations led me to conclude that my results were probably robust to this particular effect.

The activities of grizzly bears are not equally detectable. By first principles, feeding activities fall into two broad categories based on association with durable sign. Feeding that involves excavation (i.e., use of Hymenoptera, roots, rodents, rodent food caches, and whitebark pine seeds) or the manipulation of large carcasses is almost certain to be detected by a field crew. In contrast, grazing activity is likely to be overlooked because the evidence is often obscure and easily confused with grazing by ungulates. For this reason, I emphasized minimizing the commitment of a type II error, rather than a type I error, whenever I investigated a site for grazing (Mattson, 1997a). Even so, any conclusions regarding grazing were contingent on evidence (e.g., nearby feces, tracks, or beds) that a bear had at least been present. This shift in burden of proof mitigated bias against the detection of grazing compared to activities that left more definitive durable sign.

Regardless, differences in detectability among types of activities did not have a major effect on this analysis. My focus was not on estimating absolute levels of activities, but rather on explaining relative frequencies of each activity, in turn. The primary assumption of this approach was that *relative* detectabilities of activities did not change with respect to different classes, or factors, specified for activity-specific models. In other words, it did not matter if absolute detectabilities differed among activities as long as these differences did not substantially vary with type-of-bear, time-of-year, site, and ambient conditions. There was

no strong test for this assumption. However, based on my field observations and first principles, I concluded that substantial and systematic changes in relative detectabilities probably were uncommon.

Non-dietary effects on movements, morphology, and female reproduction

A large part of variation in movements of females was explained by their annual physiological and multi-annual reproductive cycles, especially in contrast to males. This may have reflected the extent to which exigencies of providing security and nourishment for dependent young dictated not only the movements, but also the growth and condition of female bears (Ramsay *et al.*, 1992; Arnould & Ramsay, 1994; Samson & Huot, 1995; Farley & Robbins, 1995; Atkinson *et al.*, 1996). As might be expected with seasonal variation in breeding activity and the impetus to feed (Nelson *et al.*, 1983), females moved farther over a larger area during Hyperphagia especially compared to movements during Estrus. Consistent with previous results (Nagy & Haroldson, 1990; Blanchard & Knight, 1991), females with COY moved shorter distances than other females within ranges comparable in size to the large ranges of subadults. This pattern suggests limited but diffuse movements, plausibly to increase the security of vulnerable young while accommodating their restricted mobility. The weak positive relation between corpulence and presence of COY probably reflects the greater likelihood that females with abundant adipose reserves produced and preserved cubs. Adult females that were alone or with young >1 yr old also moved relatively little and maintained small ranges, especially compared to subadult females. Extensive movements by subadults are consistent with exploration and dispersal prior to developing more stable maternal ranges (Blanchard & Knight, 1991).

Except for relations between 50% range sizes and morphology, movements by males were not related to any factors examined in this analysis. Consistent with hypothesis (iv), males that were large for their age tended to move over larger areas compared to males that were small. This fits general allometric relations between size and mobility (Harestad & Bunnell, 1979), as well as the expectation that larger males would be more aggressive in their search for mates and concentrated high-quality foods such as ungulate carcasses. Such a pattern also would be expected if large size were symptomatic. If growth of males was promoted by a proteinaceous diet, males prone to move more may have had more opportunities to eat meat and thus accrete lean body mass. This follows from the fact that

opportunities to feed on ungulate carcasses during this study were widely dispersed among habitat types (Green *et al.*, 1997; Table 3). The negative relation between range size and total lean body volume undoubtedly reflects the long-range movements of smaller, younger, males associated with post-weaning dispersal (Blanchard & Knight, 1991).

Among females, age had major effects on reproduction. This was manifest both in the likelihood of producing a litter and in litter size. Interestingly, senescence was the single-most important factor determining whether a female had a singleton and had no apparent effect on likelihood of 3-cub litters. Old females also were increasingly likely to lose cubs and thus more likely to have a new litter rather than be alone or have older young. All of these patterns are plausibly associated with declining physiological or behavioral competence (Adams, 1972). Otherwise, likelihood of producing cubs was strongly contingent on age until a female reached 8 ½ years, and virtually 0 before the age of 2 ½. This fit the well-established effects of age-related physical size on age of first reproduction among bears and other mammals (Harvey & Zammuto, 1985; Derocher *et al.*, 1992; Samson & Huot, 1995). Otherwise, the likelihood of cub loss declined to a nadir at about 16 ½ yrs of age, along with the related likelihood of being accompanied by COY. This could be interpreted as the average age of maximum maternal competence among Yellowstone's grizzly bears.

Causes and consequences of dietary differences

Use of whitebark pine seeds

Consistent with hypothesis (xviii), Yellowstone's female grizzly bears used whitebark pine seeds more often than did males. This disparity was greatest during Hyperphagia, when feeding activity intensified and the targeted food – in this case, pine seeds – was of corresponding importance. Consistent with hypothesis (xi), there also were strong indications that consumption of pine seeds by females affected their reproductive success. The likelihood of observing a female with a 3-cub litter was greater in areas where females ate more pine seeds and during years following or contemporaneous with large seed crops. The likelihood that a female would produce a litter, versus not, also increased following large seed crops. These patterns are consistent with the contingency of reproductive success among female grizzly bears on the accumulation of sufficient adipose reserves, facilitated, in turn, by the consumption of fatty foods such as whitebark pine seeds. Alone, the rote energetics of using pine seeds would not explain these patterns. The energy derived from

pine seeds by bears is much less than that derived from ungulate tissue and not much, if at all, greater than the energy derived from most roots and berries (Mattson *et al.*, 1999).

The potential importance of whitebark pine seeds to the reproduction of females was also expressed in the comparative distributions of bear classes. Females with COY and older young were positively associated with areas where whitebark pine habitats were extensive. This could have resulted either from females that lived in such areas more often producing cubs or from females selecting to live in such areas when accompanied by young. The latter explanation seems less likely given that the basis for reckoning the extent of different habitat types – Bear Management Units (BMUs) – were as large as the lifetime ranges of females (Weaver *et al.*, 1986; Mattson *et al.*, 1999).

Some aspects of these results are ambiguous with respect to the effects of pine seeds on the reproduction of Yellowstone's female grizzly bears. No effect of pine seeds was evident in the analysis of reproduction based on individual animals as units of analysis. Also, it seems implausible that use of pine seeds contemporaneous to the observation of a litter would affect its size – as was suggested by the partial relation of 3-cub litters to the size of contemporaneous cone crops. I suspect that the analysis of reproduction based on individual animals did not reveal an effect of pine seeds, whereas the analysis based on annual observations did, because of patterns of annual variability in size and use of seed crops by Yellowstone grizzly bears (Mattson, Reinhart & Blanchard, 1994; Mattson & Reinhart, 1994). The proportional use of pine seeds by females varied only moderately among individuals, probably due to the strong tendency of females to heavily use pine seeds whenever a large crop was produced. Given that a large crop occurred at least once during the time that most females were monitored, they had the opportunity to 'average-out' this annual variability in their individual records, and so potentially mask the joint effects of annual and spatial variation in seed crop size.

The contemporaneous effects of seed crop on litter size might derive from effects on lactation and security from predatory bears. As suggested by theory presented earlier, fatty foods could boost the quality and quantity of milk produced by a dam and thereby increase the likelihood that a third cub would survive to be first observed by a researcher later in the year. Similarly, if survival of all siblings in a large litter was promoted by use of a dispersed food such as pine seeds (Haroldson & Mattson, 1985; Mattson & Reinhart, 1997), then a

third cub would more likely be seen, especially if the first observation of the litter occurred late. I further discuss the potential effects of dispersed versus concentrated high-quality foods on cub survival below, in connection with grizzly bear use of proteinaceous foods. Despite the effects of whitebark pine seeds on reproduction of females in the Yellowstone area, there was little or no apparent effect of pine seed use on body size, corpulence, or movements. As discussed above, the effects of diet on movements and morphology of females may have been masked by the dominant effects of intrinsic annual and multi-annual physiological and reproductive cycles.

Use of pine seeds by Yellowstone's grizzly bears was contingent on the size of current and previous years' cone crops and the extent of whitebark pine habitats. This is consistent with the effect of pine seeds on female reproduction and with previously documented relations between crop sizes and frequency of pine seeds in grizzly bear feces (Mattson *et al.*, 1994; Mattson & Reinhart, 1994). The strong, non-linear, relation of use to the extent of whitebark pine habitats also is consistent with the near restriction of whitebark pine seed consumption to this type (Table 3). Furthermore, this spatial relation suggests that loss of whitebark pine forests to the 1988 fires had non-trivial effects on the behavior of Yellowstone's grizzly bears. The severity of these effects was probably greatest in BMUs with extensive whitebark pine cover and proportionally large losses: BMUs 4, 5, 14, and 15 (Fig. 6). Initially, 20–32% of these BMUs were covered by whitebark pine forests; 24, 44, 33, and 21%, respectively, of this cover was lost in 1988 (Table 4).

Proximally, use of pine seeds by bears had what might seem to be a peculiar relation to forest structure, involving a non-monotonic response to abundance of whitebark pine and coarse woody debris, and a monotonic response to total forest basal area. These patterns can be interpreted in terms of red squirrel habitat relations superimposed on the simple effects of whitebark pine abundance. During this study, grizzly bears obtained pine seeds in >90% of instances from whitebark pine cones cached by red squirrels in middens (Mattson & Reinhart, 1994). Consequently, the number of pine seeds available to bears at any given site was jointly dictated by the abundance of whitebark pine and the density of red squirrels. Red squirrels preferentially locate their middens in microsites where coarse woody debris is locally more abundant (Mattson & Reinhart, 1997). Squirrels also are more abundant where there is greater unit area production of arboreal seeds, which is positively correlated with

forest basal area (Mattson & Reinhart, 1997). At the same time, squirrels at high elevations in the Yellowstone area are less common where whitebark pine is abundant and comprises a large fraction of the forest overstory (Reinhart & Mattson, 1990b; Mattson & Reinhart, 1997). Whitebark pine betokens some of the harshest ambient environments for squirrels (Mattson & Reinhart, 1990) and, in pure stands, produces seeds erratically (Weaver & Forcella, 1986; Morgan & Bunting, 1992). This leads to cyclic, often low-density, squirrel populations (Kendall, 1983; Reinhart & Mattson, 1990b; Mattson & Reinhart, 1997). Consequently, sites with moderate amounts of coarse woody debris, moderately abundant whitebark pine, and substantial total forest basal area engender optimal conditions for bears that translate into high densities of squirrel middens containing moderate numbers of whitebark pine cones.

Use of whitebark pine seeds affected the frequency with which Yellowstone's grizzly bears engaged in other activities. All else equal, bears were less likely to excavate osmorhiza roots or ants from logs when pine seeds were abundant. They also were less likely to graze graminoids during Spring and Estrus following a large seed crop the previous year or use ungulate carrion during Spring in areas with extensive whitebark pine forests. Ant use occurred at elevations much lower than use of whitebark pine seeds, for reasons probably related to ant abundance (see below). Even so, proximal factors did not screen out all the effects of seed crop size, suggesting that bears were not using ants even when exposed to conditions that would otherwise favor this activity. Bears using pine seeds probably consumed fewer ants excavated from logs because ants returned comparatively little energy under such conditions (Mattson *et al.*, 1999). Less frequent use of the available carrion by bears in areas with abundant whitebark pine plausibly was due to a decreased impetus to feed during Spring because of greater access to pine seeds during Hyperphagia (Mattson, 1997b).

The reasons why grizzly bears dug osmorhiza roots and grazed graminoids less often when pine seeds were abundant are not self-evident. Again, the explanation could involve the relatively low quality of both these foods. Among roots, osmorhiza offered less energy to bears than either yampa or biscuitroots, while grazing offered even less energy than osmorhiza (Mattson *et al.*, 1999). Use of osmorhiza peaked seasonally at the same time as use of whitebark pine seeds. As expected by optimal foraging theory (Stephens & Krebs, 1986), bears simply may have dropped this food from their diet when a higher-quality food

such as pine seeds was abundant. Something similar could have happened when grizzly bears had option to use over-wintered pine seeds during June and late May (Mattson *et al.*, 1994) – the time of year they would otherwise most likely graze graminoids.

All else equal, grizzly bears more often bedded or used mushrooms and ungulates during years when whitebark pine seeds were abundant. They also more often used biscuitroots the following Spring and Estrus, especially in areas with extensive whitebark pine forests. The positive association between use of pine seeds and biscuitroots probably arose because of a positive spatial correlation between sites where bears obtained the two foods. Biscuitroots are typically excavated on rocky convex ridges, often at elevations >2100 m (Mattson, 1997c). Whitebark pine is similarly distributed above 2100 m on convex to uniform topography (Despain, 1990; Mattson & Reinhart, 1990). Thus, contrary to naïve predictions of foraging theory, it is likely that grizzly bears mixed digging biscuitroots during June and July with exploiting pine seeds over-wintered from a large crop the previous year.

Similar to biscuitroots, grizzly bears apparently consumed mushrooms on sites near where they consumed pine seeds. This is suggested by the positive association of mushroom foraging with whitebark pine basal area. Indeed, many of the mushrooms used by Yellowstone's grizzly bears were associated with the two most common species of pine – lodgepole and whitebark (Mattson, In prep.). Even so, while frequency of mushroom use increased during good seed crop years, the number of mushrooms dug at a site declined. This could have been caused by fewer available mushrooms at the high elevations typical of where feeding on whitebark pine seeds occurred or by diminished impetus to feed on mushrooms when pine seeds were abundant. The former explanation seems more likely based on personal observations of the limited extent of sites favorable to digging mushrooms in whitebark pine forests.

The positive association of bedding and late-season ungulate use with large whitebark pine crops is not readily explained. In fact, previous results suggested that use of ungulates during Hyperphagia was negatively related and compensatory to use of whitebark pine seeds (Mattson, 1997b). Proximally, bedding also is identified with consumption of ungulates, not pine seeds. Even so, elk were still on high-elevation summer ranges when most grizzly bears used pine seeds, August–October. Elk use of forested habitats, including stands with whitebark pine, also peaks at this time (Cole, 1969; Long *et al.*, 1980; Edge, Marcum &

Olson-Edge, 1987). Like bears, elk sometimes forage heavily on mushrooms, primarily in pine-dominated forests (Collins, Urness & Austin, 1978; personal observation). Collectively, the move by elk into forested habitats to forage on foods that potentially included mushrooms could explain the concurrent increase in use of ungulates by bears at a time when the bears themselves were in forests also consuming mushrooms along with pine seeds.

Use of ungulates and other proteinaceous foods

The apparent consequences of grizzly bears using proteinaceous foods do not yield straightforward conclusions regarding the research hypotheses posed in the introduction. Consistent with hypotheses (ii), (xvi), and (xix), males more often ate ungulates compared to females, but only during Hyperphagia. However, during Hyperphagia, more fat was available from ungulate carcasses due to the seasonal accumulation of adipose reserves by ungulates (Mattson *et al.*, 1999), and the amount of tissue obtained by a bear was much greater, on average, compared to during Spring and Estrus. Larger meals this time of year followed from the use of comparatively larger-bodied carcasses and the prevalence of predation versus scavenging (Mattson, 1997b). Compared to females, male bears consequently appropriated more feeding opportunities that consisted of large concentrations of both protein and fat at a time of year when high concentrations of dietary fat and energy predictably contributed most to accumulating adipose reserves (Nelson *et al.*, 1983). The late-season differential in ingestion of protein between the genders may partly explain why, compared to females, male grizzly bears exhibited greater growth in lean body volume during the active season.

Males and females consumed ungulate tissue with about equal frequency during Spring and Estrus. This was at a time when meals from ungulates tended to be smaller, more numerous, and comprised mostly of protein (Mattson, 1997b; Mattson *et al.*, 1999). Bears obtained less from ungulate carcasses during the early season either because of intense competition from other scavengers such as coyotes (*Canis latrans*) for tissue from winter-killed animals or because live ungulates vulnerable to predation consisted mostly of small-bodied elk calves (Gunther & Renkin, 1990; Green *et al.*, 1997; Mattson, 1997b). Nonetheless, the smaller size and greater number and dispersion of meals available from ungulates early in the year probably created more opportunities for females to find and maintain prerogative on such meals in the face of competition from males. This is especially

likely given the strong tendency for larger carcasses to attract more bears, including dominant males (Mattson, 1997b; Craighead *et al.*, 1995). It also is worth noting that, compared to males, females used higher elevations early in the year. There were greater numbers of carcasses at lower elevations during Spring (Houston, 1978; Green *et al.*, 1997), suggesting that males still dominated the best scavenging opportunities this time of year. Nonetheless, elevational partitioning probably yielded more opportunities for females to use meat at higher elevations. Consistent with hypotheses (xvi) and (xx), females probably had, and took, more opportunities to use this high-energy-content food early compared to late in the non-denning season.

Increased loss of COY by females that more often ate proteinaceous foods was the strongest and most consistent effect of diet or activity on reproductive success of females. Interestingly, there also was evidence that cub loss increased with use of fatty foods other than whitebark pine seeds. These kinds of proteinaceous and fatty foods were spatially and temporally concentrated as were the bears attracted to them. This was true for ungulate carcasses (Craighead *et al.*, 1995; Green *et al.*, 1997; Mattson, 1997b), spawning cutthroat trout (Reinhart & Mattson, 1990a; Mattson & Reinhart, 1995), and army cutworm moths (Mattson *et al.*, 1991b; French *et al.*, 1994; O'Brien & Lindzey, 1998). This increased likelihood of cub loss is consistent with the hypothesis that conspecific killing of COY increased when they were exposed to concentrations of other bears, especially adult males (Stringham, 1983; McLellan, 1994; Swenson *et al.*, 1997). Indeed, the few instances of known or suspected conspecific killing during this study occurred among bears concentrated to feed on a high-quality food (Mattson *et al.*, 1992b). Although use of proteinaceous foods could have boosted cub production, very likely any such gains would have been offset by the increased likelihood of subsequent losses.

Consumption of ungulate tissue by Yellowstone's grizzly bears was strongly related to numbers of dead, but not live, ungulates. As expected from previous research (Green *et al.*, 1997; Mattson, 1997b), grizzly bear use of ungulates during Spring — primarily by scavenging — was contingent on numbers of ungulate carcasses rather than sizes of ungulate populations. In other words, 'availability' was dictated by winter kill and was insensitive to numbers of live ungulates occupying grizzly bear range. The effects of carrion availability carried over into Estrus, with bear use of ungulates remaining comparatively frequent when

ungulate die-offs were large. Large die-offs apparently swamped scavengers (Green *et al.*, 1997), resulting in the continued availability of carrion into late May. The lack of association between numbers of live ungulates and frequency of use by bears affirms the absence of any trend in use first observed by Mattson (1997b), despite increasing elk and bison populations. This insensitivity to numbers of ungulates, as such, probably reflects the extent to which other factors affect vulnerability of elk and bison to bears, especially during Estrus and Hyperphagia.

The pervasive effect of cumulative growing season ppt on grizzly bear use of ungulates is intriguing. Greater ppt was associated with greater use during Spring and Estrus and lesser use during Hyperphagia. Very likely, greater ppt during April through mid-July resulted in either or both greater vulnerability of elk to predation by bears or a later median date of spring die-off. Greater Spring and early summer ppt, often in the form of snow, has been associated with prolonged deficit foraging, greater energetic demands, and a resulting prolongation of elevated death rates among ungulates (Meagher, 1976; Turner *et al.*, 1993). Late-Spring carrion was especially beneficial to bears because most bears were not out of their dens and active on ungulate winter ranges until April (Green *et al.*, 1997). Ungulates that died before late March were essentially unavailable. Inclement Spring and early-summer weather also could have rendered elk calves more vulnerable to predation by grizzly bears. Predation on elk calves is the most frequent means by which bears obtain ungulate meat during Estrus (Mattson, 1997b). Prolonged severe weather often results in late-born lightweight calves that are more vulnerable to predation (Thorne, Dean & Hepworth, 1976; Singer *et al.* 1997), potentially leading to more frequent use of these ungulates by bears.

Continuation of wet weather through Hyperphagia could have reduced the frequency of ungulate use by grizzly bears by affecting the distribution and/or vigor of ungulates. Wet weather can lead to dispersal of ungulates at lower elevations by prolonging the succulence and related quality of forage on such sites (Marcum & Scott, 1985). Grizzly bears do not intensively use lower elevations during Hyperphagia. High quality forage also predictably leads to improved condition among ungulates, which could reduce their vulnerability to bear predation or death due to injury during the rut. Both are especially common means by which grizzly bears obtain ungulate meat during Hyperphagia (Mattson, 1997b).

Use of carrion by grizzly bears during Spring appeared to affect subsequent use of other foods. Bears were less likely to excavate pine seeds or graze clover, and more likely to graze early-season graminoids or excavate ants from logs during years when carrion was abundant. Inasmuch as scavenging of carrion was less common in areas with extensive whitebark pine forests, use of whitebark pine seeds reciprocally declined during years when carrion was abundant. This two-way effect is consistent with the high nutritional quality of both ungulate carrion and whitebark pine seeds, despite substantially different nutrient compositions and the lower net energetic benefits of using whitebark pine seeds compared to Spring carrion (Mattson *et al.*, 1999). Such trade-offs between two high-quality foods suggest that grizzly bears may be operating to some extent as time minimizers; i.e., as long as they can meet minimum requirements for energy and nutrients by consuming some high-quality food, they will engage in other activities focused on lower-quality foods in safer environments.

Clover was the highest-quality, highest protein-content food commonly grazed by Yellowstone's grizzly bears (Mattson *et al.* 1999). It also was grazed by concentrations of bears in highly restricted patches (Graham, 1978), with attendant risks of injury or death from other bears (Mattson *et al.*, 1992*b*). As such, bears may have grazed clover partly as a mid-summer remedy to protein deficits incurred when carrion was scarce during Spring; and easily foregone because of associated risks when protein was earlier abundant. Again, such trade-offs suggest that grizzly bears were time minimizing when meeting their dietary protein requirements.

Ants from logs probably returned the least energy to grizzly bears of any food (Mattson *et al.*, 1999). Use of ants from logs peaked during July and August, about two months after grizzly bears had finished using carrion. It could be that a high-quality diet during Spring subsidized later use of a low-quality food, yet this is contrary to the tenets of foraging theory and the decline in use of ants when pine seeds were abundant. It may simply be that bears more often used ants from logs because they were more often exposed to favorable conditions as a consequence of *not* grazing clover or excavating pine seeds in characteristic non-forest and high-elevation sites, respectively. This interpretation is consistent with the fact that proximal conditions screened out the effects of ungulate carcass

abundance, suggesting increased exposure to conditions favoring the use of ants rather than increased acceptance of ants, all else equal.

Elk densities may have affected grizzly bear diets by affecting abundances of other foods. The likelihoods that dandelions, elk thistles, and graminoids were grazed by bears increased with numbers of elk. Similarly, use of thistles, clovers, dandelions, and early-season graminoids was greater in areas with either extensive low-elevation or extensive high-elevation elk winter ranges. Dandelions and thistles are known to increase with heavy grazing and associated trampling (Stubbendieck, Hatch & Kjar, 1982; Oosterveld, 1983; Mattson, 1984; Klinkhamer & De Jong, 1993). There also is good evidence that grazing by elk and bison in Yellowstone Park promoted production of graminoids, at least on ungulate winter ranges (Frank & McNaughton, 1993; Singer, 1995). Furthermore, grazing of green tissue from graminoids is facilitated by the removal of cured or dead material remaining from the current or previous year (Freer, 1981; Hodgson, 1986). Elk likely promoted grazing by grizzly bears by creating conditions leading to increased abundances of dandelions and thistles, and both increased abundance and availability of spring- and fall-green graminoids. This interpretation is consistent with proximal abundances of thistles and dandelions, but not graminoids, screening out almost all effects of ungulate numbers. In other words, Yellowstone's grizzly bears were likely eating more dandelions and thistles because of increased exposure to these foods whereas they were likely eating more graminoids because of increased green leafy biomass and efficiencies of grazing existing plants.

Contrary to the heightened use of foods associated with elk densities, bison numbers were associated with reductions in use of a host of foods, including grazing of clover, thistle, and early-season graminoids, excavation of ants from hills and pine seeds from squirrel middens, and browsing of berries. The simplest explanation is that grizzly bears less often sought out and ate these foods in areas where and at times when bison were abundant. This suggests central role for bison in the diet of Yellowstone's grizzly bears, consistent with previously-documented disproportionally intense use of bison carcasses by bears (Green *et al.*, 1997; Mattson, 1997b).

However, to the extent that proximal features screened out the effects of bison numbers, it may be that bison affected bear use of these foods by affecting abundance or quality. Such screening was the case for all but early season graminoids. Given that bison

do not browse berry-producing shrubs and rarely use elevations at which whitebark pine is abundant (Meagher, 1973), it is unlikely that bison directly affected berries or pine seeds. More likely, bears chose not to as often seek out sites where berries and pine seeds were common when they had greater potential access to bison meat. Similarly, even when proximal conditions otherwise favored grazing, bears less often chose to use graminoids during Spring and Estrus at times when and places where bison were most abundant. On the other hand, bison likely depressed bear use of clover by affecting the quality of this food. Clovers used by bears typically occurred in restricted swards also heavily used by elk and bison (Graham, 1978). Unlike elk, bison intensively grazed these patches during times when grazing by bears also was most intense; elk typically deferred their use until later in the season (unpublished data). Greater numbers of bison plausibly led to decreased clover biomass and, thus, to decreased use of clover by bears.

Early-season use of rodents or their food caches by grizzly bears was positively associated, proximally and distally, with greater numbers of bison. Bison could have caused increased use of rodents by bears through indirect effects on numbers or vulnerabilities of pocket gophers. In fact, bison can boost pocket gopher populations by creating favorable gopher habitats (Steuter *et al.*, 1995). Also, bison numbers could have affected the motivation of bears to use rodents on bison ranges, much like the apparent positive effect of pine seed use on use of nearby biscuitroots. Such effects imply opportunistic, if not subsidized, use of lower quality foods near high-quality ones. More specifically, given that subadults used early season rodents more intensively than did adults, use of rodents might have mitigated the costs to these subordinate bears of being active in an area primarily to exploit the uncertain opportunities for scavenging bison in the face of competition from dominant bears. These possible effects, plus others involving the abundances of thistles and ants in non-forest habitats, suggest a keystone role for bison in areas shared with grizzly bears.

Proximally, conditions associated with grizzly bear use of ungulates changed between seasons, partly as a consequence of changes in habitats used by ungulates. During Spring, grizzly bears were most likely to scavenge ungulates on sites with sparse vegetation ground cover, few live mature trees, and near a forest/non-forest edge. This vegetation structure is typical of patchy barren geothermally-influenced sites that comprised a substantial part of the

bison and elk winter range used most heavily by Yellowstone's grizzly bears for scavenging winter-killed ungulates during Spring (Green *et al.*, 1997). After Spring, grizzly bears were most likely to prey on or scavenge ungulates on sites with abundant forbs that were far from a forest/non-forest edge. This occurred more often in forested stands during Estrus, and in more open conditions typified by abundant grass during Hyperphagia. The association with forbs during Estrus fits the kinds of sites where grizzly bears often killed elk calves (French & French, 1990; Gunther & Renkin, 1990) – a dominant activity during Estrus (Mattson, 1997b). Similarly, the strong association of use during Hyperphagia with graminoid-dominated sites far from forest cover fits the kinds of sites where bears often scavenged bull bison that died from injuries sustained during the rut.

Use of roots

Most roots offered Yellowstone's grizzly bears either less energy or less concentrated fat or protein compared to whitebark pine seeds and ungulate tissue (Mattson *et al.*, 1999). This relative paucity of highly digestible nutrients was reflected in smaller sizes of females and lesser corpulence of males that ate large amounts of roots. Males were thin despite moving less while eating roots compared to while eating other foods. The restricted movements of bears using roots, inferred from aerial telemetry, matched what was observed during close monitoring (Schleyer *et al.*, 1984; Haroldson & Mattson, 1985; Harting, 1985). As expected by their smaller size, and consistent with hypothesis (xxi), females that consumed more roots were less likely to have litters of ≥ 3 cubs, especially compared to females that ate more pine seeds. As speculated elsewhere (Pearson, 1975; Russell *et al.*, 1979; Hamer & Herrero, 1987), these results suggest that roots often were used by grizzly bears to compensate for a dearth of higher-quality foods, with diminished size, condition, and reproductive success for the involved bear. Even so, roots are a defining feature of grizzly bear diets (Herrero, 1978; Mattson, 1998), and a food that conceivably allows this species to exist at densities that would otherwise not be possible by mitigating against endemic variation in abundance of higher quality foods.

The effects of size-of-bear on use of roots were ambiguous with respect to hypothesis (xxi). In contrast to females, males rarely used yampa roots. In fact, abundance of yampa contributed substantially to distinguishing sites used by adult females from sites used by adult males. At the same time, larger bears (adults) used biscuitroots more often than did

smaller bears (subadults). No effect of bear size was evident in use of *osmorhiza* roots. There is no unequivocal explanation for these patterns. However, biscuitroots tended to be larger and more easily dug than yampa roots, especially during Hyperphagia (Mattson *et al.*, 1999). Adult males also tended to spend more time in areas with extensive rocky convex ridges — sites highly favored by bears for excavation of biscuitroots (Mattson, 1997c; Table 3). It could be that adults dug more biscuitroots because easier digging and the greater energetic reward offered by larger roots offset the geometric increase in energy expense entailed by larger excavations by a larger paw.

Males more often than females choose *not* to dig yampa roots even when exposed to favorable proximal conditions. This further suggests gender- rather than size-related effects on grizzly bear use of this root food. Even so, bear size could have had an indirect effect if females choose more often to dig yampa when accompanied by dependent young so as to optimize energy gain and security for the family group. Cubs would have had an opportunity to dig a root food well-suited to their small size in a habitat little-used by adult males. Frequent excavation of yampa roots by lone adult females could simply have been a pattern developed while they were subadults and reinforced the other 2 years of a 3-yr reproductive cycle (Herrero, 1985; Meagher & Fowler, 1989; Gilbert, 1999).

Use of all three roots was contingent on the proximal abundance of each and on amounts of recent or cumulative precipitation. The relationship between likelihood of use and proximal abundance differed among the species as a probable consequence of differences in habitat distributions and related foraging behavior by the bears. A strong sigmoidal relation with an asymptote approaching 1 — as for biscuitroots — suggested that grizzly bears were orienting towards sites where this root plant was abundant only at times when the bears were using this food. A bear was almost certain to dig biscuitroots when exposed to even moderate densities, otherwise not. This pattern arose partly because such food plants were distributed in restricted habitat types not much used for other foraging activities, as was true for biscuitroots (Table 3). This was less the case for yampa and *osmorhiza* roots. Grizzly bears frequently were exposed to high densities of these roots without digging them, which followed, in part, from the broader distribution of these species in habitats used by bears for other activities (Mueggler & Stewart, 1980; Steele *et al.*, 1983; Mattson, 1984; Table 3).

The contingency of root use on advanced phenology and periods of greater precipitation is not surprising. Shear strength diminishes considerably when soils are moist (Hillel, 1980), thereby predictably increasing the net energy derived from digging roots. This would explain the positive relation between contemporaneous rainfall and likelihood of use for all three root foods. Similarly, advanced phenology entails a greater reward for bears. Starch content of roots is at its annual nadir during active shoot growth, prior to anthesis (Mattson, in prep.). By and after anthesis, starch content peaks in yampa and biscuitroots and remains high for the remainder of the growing season. Consequently, Yellowstone's grizzly bears were most likely to consume roots when conditions were optimal for minimizing energetic costs (wet soils) while maximizing energetic benefits (peak digestibility and starch content) – a general result in agreement with more detailed studies of use of biscuitroots by grizzly bears (Mattson, 1997c).

Use of rodents and rodent food caches

The positive association of corpulence among females with late-season use of rodents was probably symptomatic rather than causal. Use of fossorial rodents by grizzly bears during Hyperphagia was positively associated with bedding and use of roots and potentially indicated the effects of a suite of activities more than its effects alone. Bears also derived comparatively little net energy from rodents or their food caches (Mattson *et al.*, 1999). Moreover, use of fossorial rodents and their foods during Hyperphagia was comparatively rare. Thus, the energy, nutrients, or behaviors entailed by late-season use of fossorial rodents are not plausibly invoked as leading to greater corpulence. More likely, females that were more corpulent turned more often to digging rodents, along with roots, during Hyperphagia. Among reproducing females, adipose reserves may have subsidized use of these dispersed lower-quality foods as a means of minimizing risks from other adult bears to self and dependent young.

Excavation of rodents and their food stores by bears was affected by year-round weather. As with roots, greater contemporaneous rainfall led to greater likelihood of use and larger excavations during Hyperphagia, no doubt because of greater ease of digging. Conversely, greater winter ppt and progression of the growing season were associated with a decreased likelihood that rodents would be pursued by bears during Spring and Estrus. These effects of date and winter ppt could be associated with conditions favoring the capture of

rodents and their food stores by bears. Optimal conditions likely occurred when the vulnerability of rodents was elevated by saturated snow-free soils (Ingles, 1952; Youmans, 1979) and when rodents and their food caches were abundant. With deep snow, snow melt would take longer, causing attrition of rodents and their food stores (Turner *et al.*, 1973; Chase, Howard & Roseberry, 1982). Deep snow also predictably entailed increased expenditure of energy by bears pursuing rodents. Consequently, compared to years of light snowfall, heavy winter ppt probably yielded fewer rodents or rodent food caches once snow melt occurred as well as greater amounts of alternate higher-quality foods such as ungulate carrion (see above). Regarding the negative relation during Hyperphagia between use of rodents and cumulative growing season precipitation, there is not enough known about how weather affects post-Spring pocket gopher survival to speculate. However, as with effects during Spring and Estrus, the explanation likely involves both rodent densities and vulnerabilities.

Excavation of rodents or rodent food caches by Yellowstone's grizzly bears occurred disproportionally often in mesic or wet non-forest sites. This matches the habitat relations described for pocket gophers and most voles in mountain environments (Findley, 1951; Hodgson, 1970; Turner *et al.*, 1973; Youmans, 1979; Chase *et al.*, 1982), and is consistent with bears seeking out rodents in areas where they were most abundant. In contrast to Spring and Estrus, during Hyperphagia grizzly bears more often and more extensively dug for pocket gophers and voles in wet non-forest sites typified by abundant sedges. This probably reflected higher densities of rodents on such sites later compared to earlier in the growing season (Hodgson, 1970; Youmans, 1979; Chase *et al.*, 1982), as well as continued ease of digging in wet-site soils.

During Spring and Estrus, there were positive relations between the abundance of yampa at a site and both the likelihood of digging and the extent of excavations for pocket gophers by grizzly bears. Yampa roots are often part of pocket gopher food caches. The plant itself is positively correlated with pocket gopher densities late in the growing season (Youmans, 1979). Yampa also is a preferred, high-quality, root food of Yellowstone's grizzly bears (Mattson, *et al.*, 1999). The positive association between yampa abundance and early-season use of rodents by bears plausibly arose because yampa indicated greater densities of pocket gophers as well as the occurrence of higher-quality rodent food caches.

Wheatgrass (*Agropyron caninum*) was positively associated with the rate at which grizzly bears encountered nests and food caches of pocket gophers or voles in their excavations during Hyperphagia. These relations can be explained by the strong positive association between wheatgrass and high densities of pocket gophers (Turner *et al.*, 1973; Laycock & Richardson, 1975; Youmans, 1979). Wheatgrass is not eaten by gophers or voles and apparently increases in abundance as prolonged exploitation of forbs by high densities of pocket gophers reduces competition and allows for the establishment and spread of grasses (Ellison & Aldous, 1952). Wheatgrass consequently indicates sites with a comparatively long history of high rodent densities. The negative association between rate of encounter with food caches by bears and onion grass (*Melica spectabilis*) abundance is consistent with this interpretation. Unlike wheatgrass, onion grass is a preferred gopher food that has been observed to decline with increased gopher densities (Turner *et al.*, 1973). Thus, sparse onion grass also could indicate a long history of high pocket gopher densities.

Use of ants and other Hymenoptera

Ants probably offered Yellowstone's grizzly bears the least energy of any food in the study area (Mattson *et al.*, 1999), and yet were frequently consumed. This type of frequent consumption has intrigued researchers and lead to speculation regarding the potential role of insects in supplementing critical amino acids and dietary protein (Eagle & Pelton, 1983; Hamer & Herrero, 1987). Because ants seem offer so little energy, it might be surprising that females who frequently ate ants lost fewer cubs, especially compared to females who frequently ate trout or ungulates during Spring and Estrus. However, this enhanced survival can be explained in terms of the dispersion of ant-eating opportunities. Indeed, opportunities to eat ants are commonplace and widespread among forest types (Table 3). Consequently, in contrast to bears that consumed high-quality proteinaceous foods, bears that ate ants were well-dispersed (Schleyer *et al.*, 1984; Harting, 1985; Haroldson & Mattson, 1985). This probable difference in exposure to other bears plausibly led to the observed difference in survival of cubs. If so, this result is consistent with the hypothesis that grizzly bear cubs in Yellowstone were killed by other bears, but less often when females with young were using an abundant, dispersed, food such as ants.

Use of ants by grizzly bears was most likely and most extensive under conditions that logically promoted ant abundance. These conditions consisted of abundant substrate suitable

for ant nests, coupled with warm ambient conditions. For ants in logs, optimal conditions and associated peak bear use occurred where there was moderately abundant large-diameter coarse woody debris under an open forest canopy (Sanders, 1964, 1970; Torgersen & Bull, 1995; Kidd & Longair, 1997), at lower elevations during the warmest months of the year. Although well-decomposed debris probably did not promote ant abundance (Torgersen & Bull, 1995), it likely facilitated access by bears to ants contained within. For ants in dirt or debris hills, optimal conditions consisted of gently-sloping non-forest sites and the warmest months of dry years.

This analysis emphasizes the probable importance of site warmth to abundance of ants in this study area and related opportunities for bear use. The positive relation between temperatures and biomass of temperate or boreal-zone ants is well-established (Gregg, 1963; Brian, 1978; Coenen-Staß, Schaarschmidt & Lamprecht, 1980). Even with forest-dwelling ants, conditions improved where there was the least forest cover, which presumably resulted in increased incident radiation and elevated nest temperatures. Especially during warm and dry years, bear use also reflected the well-established tendency for ant populations to increase during the growing season, commensurate to increases in nest temperatures (Scherba, 1961; Sanders, 1972; Brian, 1978; Noyce, Kannowski & Riggs, 1997). At the broadest scale, this interpretation is supported by the lack of ants in diets of most brown bears at very high latitudes (Mattson, 1998), presumably as a consequence of few ants in the coldest climates (Gregg, 1963).

Use of grazed foods

Like ants, most grazed foods offered grizzly bears little energy (Mattson et al., 1999). In Yellowstone, this held especially for elk thistle and graminoids late in the growing season. Consequently, it is not surprising that female grizzly bears who more often grazed these fibrous foods had comparatively small ranges. However, for the same reasons identified for use of rodents during Hyperphagia, use of fibrous foods was more likely symptomatic than causal. As with roots, the comparatively restricted ranges associated with greater grazing plausibly were indicative of bears with spatially curtailed options resorting to use of less-preferred foods.

The frequency with which grizzly bears grazed most foods was affected in some way by weather. Thistle and dandelions were grazed most often during the warmest, wettest,

months of the study, suggesting that growth and nutrient content of these invasive or increaser species were greatest under these conditions. By contrast, bears grazed graminoids during Spring and Estrus most often during the coolest months of dry Springs, especially on sites where bluegrasses had not yet flowered. This suggests a strong preference by bears for succulent leafy growth of graminoids, typified by high digestibility and high protein content (Mealey, 1980; Hamer & Herrero, 1987; Mattson *et al.*, 1999). The positive effect of Spring dryness may simply have reflected the benefits of snow-free ground.

The lack of phenological effects on grazing of forbs by bears, in contrast to the presence of such effects in their consumption of graminoids, likely reflected differences in defenses against grazing between monocotyledons and dicotyledons. Grazers are deterred from grazing graminoids primarily by high fractions of silica and fiber, which develop as plants approach anthesis (Van Soest, 1987). On the other hand, grazers are deterred from grazing forbs primarily by spiny structures or secondary compounds, which occur in varied concentrations on or in different plant parts at different stages of growth (Barry & Blaney, 1987). This is not to say that phenology does not affect grazing by grizzly bears on any forb. For example, it is likely that there are strong phenological effects on the consumption of ephemeral forbs such as spring beauty (*Claytonia lanceolata*) and oxyria (*Oxyria digyna*). Rather, phenology did not have a strong effect on grazing of forbs investigated in this study, and seems to have more varied effects on bear use of forbs compared to their use of graminoids.

Grazing of graminoids by bears was more closely associated with bluegrass during Spring and Estrus and reedgrass during Hyperphagia. Late-season grazing also was negatively associated with wheatgrass. These patterns likely reflect the shift of grazing from open uplands to wetter, more shaded, bottomlands. The former sites are betokened by wheatgrass while the latter are betokened by reedgrass (Mueggler & Stewart, 1980; Mattson, 1984). Given that the digestibility of graminoids typically remains higher late in the growing season on wetter shaded sites compared to drier open sites (Graham, 1978), it is not surprising that grazing by bears reflected this difference.

As with roots, the form of the relation between abundance and use of grazed foods signified differences both in distributions of species and in grizzly bear foraging behaviors. Use of clover was most clearly distinguished from use of other grazed foods by the acute

sigmoidal form of a relation that approached an asymptote of 1. This pattern suggests that use of clover by bears was strongly contingent on very high densities of this plant, and almost certain to happen under such conditions. This fits the strong orientation of grizzly bears in Yellowstone to clover patches when grazing clover (Graham, 1978; Mattson *et al.*, 1992b; personal observation). Conversely, grizzly bears were often exposed to widespread and abundant dandelions and graminoids, but only choose to graze these foods at favorable times. Use of elk thistle was similarly contingent on factors other than proximal abundance, including the fact that this biennial species often occurred as ground-hugging year-old rosettes unusable to bears (Cronquist, 1994).

Effects of avoidance, competition, and population density

Habitat segregation

Yellowstone's grizzly bears tended to use different kinds of habitats depending on gender, age, and parturient status. Not surprisingly, sites used by lone adult females and subadult males were the least different from sites used by adult males. Conversely, and consistent with hypothesis (xiii), sites used by females with COY were more different from those used by adult males than any other class of bear, year-round. To a lesser extent, this also held true for females with older young. However, it was the sites used by subadult females and adult males that were most different. It is highly unlikely that wide-ranging opportunists such as grizzly bears would use completely distinguishable habitats if they lived in the same general area, yet the models presented here were able to differentiate about 40% of the sites used by adult males versus subadult females. Subadult females may have been under the least energetic duress of any class of bear (Mattson, 1990) and therefore able to maximize their avoidance of areas used by adult males.

Distal factors, especially the extent of habitat and winter range types, contributed much to the distinction between sites used by adult males versus subadult females or females with COY. As mentioned before, the extent of habitat types was reckoned on the basis of BMUs, which are about the size of female life ranges (Weaver *et al.*, 1986; Mattson *et al.*, 1999). By contrast, male ranges were several times larger than female ranges and also larger than most BMUs (Blanchard & Knight, 1991). Thus, the broad-scale differentiation between habitats used by males and females was more likely a consequence of males choosing to use regions not often used by females than a consequence of females shifting their ranges away

from males. If this were the case, then males were choosing to use areas with more extensive rocky slopes and ridges, mesic non-forest sites, and high-elevation elk winter range, while avoiding areas with more extensive whitebark pine forests and low-elevation elk winter range, at least compared to females. Rocky ridges were strongly associated with biscuitroot feeding opportunities (Table 3). High-elevation elk winter range provided either higher-quality scavenging opportunities during Spring (Green *et al.*, 1997) or, together with mesic non-forest sites, more opportunities to encounter ungulates on summer ranges (Cole, 1969; Long *et al.*, 1980; Houston, 1982; Edge *et al.*, 1987).

All females except lone adults were strongly associated with areas containing extensive whitebark pine forests. As discussed earlier, this fits the female predilection to eat whitebark pine seeds and associated gains in fitness. The differences between lone adults and all other females are difficult to interpret. They may be a consequence of females living in areas with sparse whitebark pine producing fewer litters or losing them more often compared to reproductive females living elsewhere. This explanation seems more probable than females moving long distances to use areas with fewer whitebark pine when unaccompanied by cubs. As with differences between females and adult males, it is likely that this broad-scale difference in habitat use among females resulted more from different foraging strategies and diets than from bears avoiding each other.

Compared to males of any age, females with COY tended to use higher elevations during Spring and Estrus and steeper slopes during Hyperphagia. During Spring and Estrus, females with COY also tended to use steeper slopes than other adults of the same gender, but shared a proclivity for steep slopes with other females during Hyperphagia. With the exception of lone adults, females also used sites with more forest basal area compared to males later in the year. These late-season patterns are explained, again, in terms of differential use of whitebark pine seeds. Whitebark pine is a member of forest communities and tends to grow in mountainous areas on upslopes and ridges (Despain, 1990; Mattson & Reinhart, 1990). Of all finer-scale patterns, the tendency for females with COY to use slopes steeper than those used by other adult females could be interpreted as avoidance behavior. Adults of both genders conceivably pose a threat to COY of unrelated individuals (McLellan, 1994).

These patterns and their interpretation collectively suggest that, at all scales, differences in habitat use by different classes of bears were often due to differences in habitat selection driven by different dietary preferences. Even so, there appeared to be fitness consequences for females using foods that put their cubs in harms way. Females that adopted such risk-prone strategies may have done so, and borne the consequences, because they had few other options within or near their ranges. Thus, these results do not contradict the minimal segregation among grizzly bears observed by Mace & Waller (1997), nor do they contradict the risks to COY posed by other bears speculated by Stringham (1980, 1983), Wielgus & Bunnell (1994), and Swenson *et al.* (1997). It is likely that females in Yellowstone's post-dump-closure era benefited from broad-scale segregation of the genders that naturally arose from different dietary preferences. Conceivably, these differences lead males and females to more heavily use different habitat complexes. In ecosystems where abundant high-quality foods are not nutritionally different nor distributed in different broad habitats, strategies of avoidance may be more overt or manifest on a finer scale.

Density dependence, competition, and density independence

Most researchers have either postulated or concluded from their studies that survival of most bear classes is density-dependent and that reproduction of female bears is not (*e.g.*, Bunnell & Tait, 1981). My results are seemingly consistent with density-independent reproduction because there were relations between cub production or survival and abundance or use of certain foods. Even so, Stringham (1983, 1986) suggested that reproduction among females aggregated at open-pit dumps in Yellowstone was negatively affected by density of adult males. Furthermore, Mattson *et al.* (1992), Mattson (1998), and Pease & Mattson (1999) have shown that mortality rates of Yellowstone grizzly bears can vary substantially among years in response to variation in abundance of high quality foods – a putative density-independent effect.

A deeper understanding of this dissertation's results, along with reconciliation of previous research, can come from dropping the paradigm of density-dependence. Krebs (1995) argued that density is not a mechanism, but rather a secondary phenomenon with little explanatory power. This argument is implicit to Figure 33, where key results of this dissertation and previous research on mortality rates of Yellowstone grizzly bears are synopsized. Logically, the effects of bear densities on reproduction are expressed through

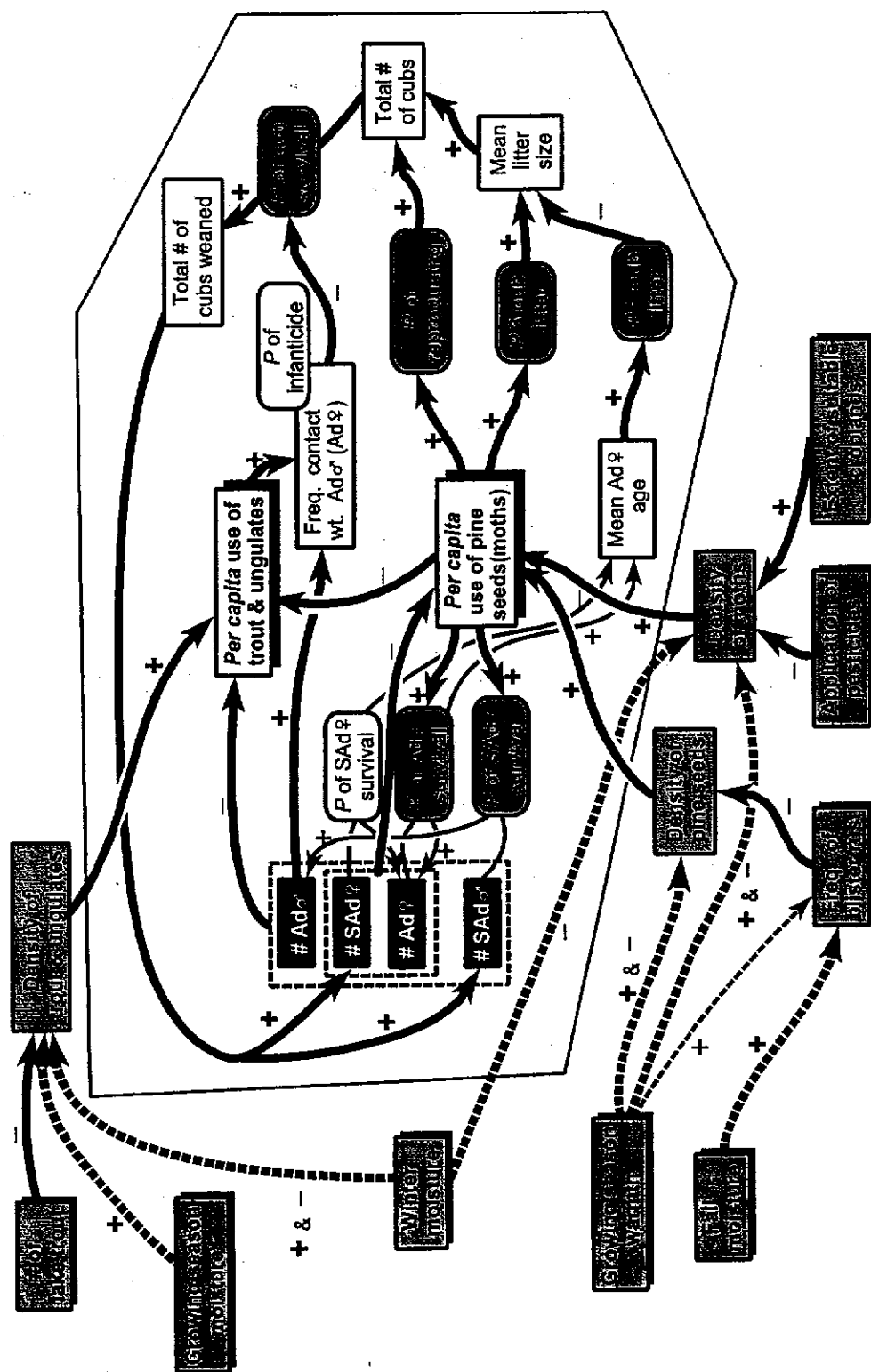


FIG. 33. A theoretical model showing density- and food-related factors and relations affecting reproduction and survival of Yellowstone grizzly bears. The polygon incloses intrinsic population processes. Demographic probabilities high-lighted by this research and Mattson *et al.* (1992) and Pease and Mattson (1999) are denoted by shaded rounded boxes. Numbers of bears in various classes (Ad = adult, SAd = subadult) are denoted in white against a black background. External food- and weather-related forcing factors are denoted by dashed lines and '+' and '-' denote the nature of the effect. Dashed lines indicate effects less direct than those indicated by solid lines. Thin lines denote a lesser effect compared to thick lines and '+' and '-' denote the nature of the effect.

per capita availability and use of whitebark pine seeds and proteinaceous foods (i.e., supply-demand ratio; Krebs, 1995; Fryxell & Sinclair, 2000) and either associated risks of infanticide or associated benefits of enhanced COY production. In other words, production and survival of COY are bound to be some function of *per capita* use or availability of critical foods, in turn a function of the joint abundance and distribution of foods and competitors, conspecific or otherwise. In keeping with the seemingly often misconstrued arguments of Andrewartha & Birch (1954: 17), the density of some class of bears is likely to influence every effect to some degree. In other words, no effect is likely to be entirely density-dependent or -independent.

The influences of food and bear densities on reproduction can be fruitfully recast in terms of the effects of distal and proximal factors. By this approach, densities of foods and densities of conspecific competitors or predators are distal factors. *Per capita* consumption of specific foods or encounters with potential conspecific predators are more proximal. Rates of accumulation of adipose reserves and rates of attacks on COY by conspecifics are more proximal yet (Figs. 1 & 2); *ad infinitum*. Density of conspecifics suffers the disadvantages of any distal factor – including broad representations of food abundance such as by proportional area of whitebark pine forests – in that its’ ultimate effects on survival or reproduction are contingent on a number intervening phenomena. Consequently, I expect that environmental factors versus bear densities have varying effects on reproduction of Yellowstone’s grizzly bears depending on specific conditions in time and space. This expectation facilitates the interpretation of some key results of this dissertation.

The best models describing putative effects of activity and female age on production and survival of COY leave much variation unexplained. I speculate that some of this unexplained variation is attributable to temporal and spatial variation in competition with conspecifics and other species. Thus, the identification of food-related effects on female reproduction in this study does not preclude effects of conspecific densities; nor does it provide support for female reproduction being wholly “density-independent.” Unfortunately, estimates of densities of various bear classes for each year and BMU were unavailable and, thus, density-related effects remain uncontrolled in the models presented above.

The combined effects of competition and food abundance likely explain the shape of most relations between probability of use and distal measures of food availability. In four of

five instances where these relations were evident (for whitebark pine seeds, ungulate use during Spring, excavation of yampa roots, and excavation of osmorhiza roots), likelihood of use increased geometrically with either indirect or direct distal measures of food abundance. I speculate that insensitivities of use at low to moderate abundances were caused by saturation of favorable feeding sites by conspecifics (interference competition) coupled with scramble competition from other species. At higher abundances, I speculate that bears escaped much of this competition as favorable patches of a given food proliferated and either exceeded collective demand or the physical limits of dominant bears to restrict access by conspecifics. This is especially likely if large inter-annual variation in abundance of key resources limited local densities of bears below levels potentially sustained at peak annual availability of any given food. Furthermore, I suspect that feedback reinforced the choice by bears to use an abundant food (Stephens & Krebs, 1986).

This interpretation is consistent with other research from Yellowstone. There is good evidence that coyotes were major competitors of grizzly bears for ungulate carrion (Green *et al.*, 1997) and that dominant bears limited access by more subordinate individuals to carcasses (Schleyer, 1983; Craighead *et al.*, 1995; Mattson, 1997b). Clark's nutcrackers (*Nucifraga columbiana*) and other seed predators also are known to consume or store a substantial fraction of whitebark pine seed crops, especially when crops are small (Hutchins & Lanner, 1982). There is no basis for judging to what extent interference competition affected grizzly bear use of pine seeds. Regardless, pine seed crops and ungulate winter die-offs varied widely among years (Table 5) and likely limited the bear population below levels that could fully exploit these foods at peak availability (Pease & Mattson 1999; these results).

The nonlinear response of use to availability of pine seeds and ungulate carrion has some important implications. For one, relations of use to availability would not have been detected if either the inter-annual or geographic extent of variation had not included high levels of availability. If availability had been limited to low or moderate levels, then I might have concluded use was not affected by availability. This conclusion argues for the importance of long-duration observational studies of large mammals spanning large geographic areas (Gaud, Balda & Brawn, 1986; Mattson, 1997c). It also argues for considerable caution when interpreting studies that do not meet these conditions. These nonlinear responses furthermore suggest that Yellowstone's grizzly bears will be most

affected by losses of foods at times and in places where these foods are currently most abundant. In other words, “surplus” high-quality foods or habitats probably do not exist.

This last point is emphasized by the nature of relations between cub production and whitebark pine seeds. As with relations between use and availability of foods, probability of producing a 3-cub litter increased geometrically with either use or availability of pine seeds. In other words, production of large litters is apparently quite vulnerable to loss of either very large seed crops or initial incremental losses of whitebark pine forests in areas where such forests currently are most extensive. This result reinforces concerns about future effects of global climate change, timber and fire management practices, and white pine blister rust (*Cronartium ribicola*).

Projected effects of environmental change

Effects of wolves

Several effects of the recent (1995) reintroduction of wolves (*Canis lupus*) to the Yellowstone ecosystem have been predicted. Among them are (1) 3–30% declines in populations of elk, moose, and mule deer, (2) declines in numbers of coyotes, (3) more even annual mortality of ungulates, resulting in less winter kill and more summer–fall carrion, and (4) potentially severe reductions in numbers of elk wintering in small high-elevation geothermally-influenced winter ranges (Singer, 1990; Singer & Mack, 1992; Boyce & Gaillard, 1992; Garton *et al.*, 1992). Of these predicted effects, declines in coyote populations have been confirmed (Smith, Brewster & Bangs, 1999; Crabtree & Sheldon, 1999), although kill rates of elk have been somewhat higher than predicted (Smith *et al.*, 1999). The reduction and even elimination of elk from small high-elevation winter ranges (*e.g.*, Heart Lake) also has been documented (D. Reinhart, Yellowstone National Park, Wyo., personal comm.). These observations, together with results of this dissertation, provide a basis for refining the appraisal by Servheen and Knight (1990) of potential future effects of wolves on grizzly bears in the Yellowstone ecosystem.

Seasonal opportunities for grizzly bears to scavenge ungulate carrion likely will change. All else equal, competition with coyotes for ungulate carrion should decline for grizzly bears, especially in northern parts of Yellowstone National Park. This is where competition with coyotes for Spring carrion was most intense prior to restoration of wolves (Green *et al.*, 1997). Even so, there will likely be fewer winter-killed elk. Competition with

wolves for carrion also will increase. More certainly, it appears that grizzly bears have been deprived of Spring carrion in high-elevation geothermally-influenced winter ranges where historically this food was most intensively used by bears (Green *et al.*, 1997). In toto, it seems more likely than not that grizzly bears will have access to less Spring carrion with wolves compared to without. On the other hand, grizzly bears should have access to more carrion from elk and deer killed by wolves during Estrus and Hyperphagia. Thus, grizzly bears will potentially scavenge more during Estrus and Hyperphagia and less during Spring with wolves compared to without.

This seasonal shift in scavenging opportunities together with likely reductions in total amounts of Spring carrion will likely benefit male more than female grizzly bears. Females consumed the most ungulate tissue during Spring, presumably because the abundance and dispersion of carrion this time of year allowed for greater partitioning of scavenging opportunities between the genders. Reduced Spring carrion would predictably diminish opportunities for females to scavenge. Moreover, this reduction could be substantial given that most change in bear use of Spring carrion occurred at the highest counts of ungulate carcasses (see above). Compounding this Spring scenario, males are better than females at exploiting late-season opportunities to consume ungulates. This is probably a consequence of their higher kill rates (Mattson, 1997b) and ability to dominate scavenging of larger-bodied carcasses (Schleyer, 1983; Craighead *et al.*, 1995; Mattson, 1997b). These assets more likely than not will also allow males to dominate opportunities for scavenging wolf kills during Estrus and Hyperphagia. Unless these opportunities saturate demand by adult and large subadult males, females probably will not benefit from increased late-season carrion.

Even if females obtained more ungulate tissue directly or indirectly because of wolves, the benefits are unclear (see above). There is no evidence for an increase in female reproduction with increased consumption of ungulate tissue. However, even if such an effect did exist, there is stronger evidence for females who consume more meat losing more of their cubs compared to females who eat more of other foods. There is no reason to think that this risk would diminish if females accompanied by young were competing with wolves and large male grizzly bears for late-season opportunities to scavenge wolf kills. On the other hand, if Spring use of carrion did contribute to maintaining cub production at levels observed during

this study, diminishment of this seasonal food could reduce female reproduction. Although wolves probably will not have a dramatic impact on Yellowstone's grizzly bears, it is much more likely that net effects will be neutral or negative rather than positive.

Effects of climate change and fire

Global climate warming is happening (Hansen *et al.*, 1998; Kerr, 1998), with anticipated major effects on the abundance and distribution of foods used by Yellowstone's grizzly bears (Romme & Turner, 1991; Bartlein, Whitlock & Shafer, 1997). Although increased temperatures are virtually certain, there is yet no confident prognosis for precipitation and growing season soil moisture in the Yellowstone area. Even so, the frequency and extent of wildfires are expected to increase as a consequence of increased drought and, in places, abundance of fuels (Romme & Turner, 1991; Price & Rind, 1994; Bartlein *et al.*, 1997; Stocks *et al.*, 1998). Results of this and other studies provide a basis for anticipating some of the consequences to Yellowstone's grizzly bears of these expected changes.

There is evidence from this study that grizzly bear foraging is temperature and moisture sensitive. The abundance and related use of ants by grizzly bears clearly seem to be dependent on ambient warmth as, to a lesser extent, do growth and use of dandelions and thistles. It is likely that use of these foods by bears will increase with climate warming, assuming that moisture relations remain unchanged. However, use of many vegetal foods was sensitive to amounts of ppt. The likelihood that bears would excavate a food declined during dry months, as did the likelihood that they would graze many of the forbs and grasses. All else equal, it is likely that grazing and root grubbing would be less common if climate warming caused drier soils during the growing season. In addition, the sensitivities of grubbing for biscuitroots and rodents to total winter ppt suggest that use of biscuitroots would decline and use of rodents would increase if winters became drier.

Currently, it is strictly a matter of speculation whether total amounts of vegetal foods would change in bear range, aside from whether these foods would be used by bears or not as a function of proximal conditions. Compared to use of biscuitroots, use of yampa is conceivably more sensitive to widespread drying because yampa is restricted to moist sites (Mueggler & Stewart, 1980; Mattson, 1984) and is typically more difficult to extract (Mattson *et al.*, 1999). It also is likely that consumption of clover by Yellowstone's grizzly

bears will be more sensitive to changes in ambient conditions than many other bear activities because use of this food is so strongly associated with dense swards on moist soils.

Otherwise, use of mushrooms and *Shepherdia* may increase because bear use of these foods is strongly linked to low-elevation lodgepole pine-dominated types (LPICO and LPIEN; Table 3). These types will likely become more extensive under warmer conditions (Romme & Turner, 1991).

Fire had a number of effects on the behavior of Yellowstone's grizzly bears that would likely ramify if climate warming induced more frequent and extensive burns. Grizzly bears were more likely to graze dandelions and early-season graminoids after the 1988 wildfires compared to before. On the other hand, the likelihood that they would excavate osmorhiza roots or whitebark pine seeds declined substantially along with the intensity of excavations for pine seeds. The former activities were more likely to occur in recent burns, while the latter were not (Blanchard & Knight, 1990; Mattson, 1997a; Table 3). All of these consequences are logically related to fire-caused increases or declines in these foods (Blanchard & Knight, 1990; Singer & Harter, 1996; Mattson, 1997a). The post-1988 decline in bear use of rodents and rodents food caches during Spring and Estrus could have been a consequence either of fire-caused pocket gopher mortality or bears choosing to graze instead. Unfortunately, there is little research on the consequences of fires to pocket gophers that might provide insight into which was a greater effect. Even so, the increase in post-fire use of rodents during Hyperphagia suggests that pocket gopher mortality was not a factor and that the explanation lies in trade-offs with opportunities to graze graminoids, year-round.

Longer-term, the abundance of whitebark pine is projected to decline substantially with climate warming as its high-elevation distribution becomes increasingly restricted (Romme & Turner, 1991; Bartlein *et al.*, 1997). Some models have suggested that increased fire leads to increases in whitebark pine (*e.g.*, Keane *et al.*, 1990, 1996), but these efforts have not considered the progressive truncation of whitebark pine distribution at lower elevations by early-successional competition with other tree species such as lodgepole pine and Douglas-fir that would likely occur as the climate warmed (Mattson, Kendall & Reinhart, In press). Results from this study confirm previous investigations (Blanchard & Knight, 1990; Blanchard & Knight, 1996) showing that stand replacement fires in whitebark pine forests lead to potentially major short-term declines in the use of pine seeds by Yellowstone's

grizzly bears. As noted above, these declines include not only reduced frequency of use, but also reduced sizes of excavations. Smaller excavations are probably a consequence of diminished midden sizes resulting from increased packing of red squirrels in unburned forest patches (Mattson *et al.*, In press; Podrutzny, Reinhart & Mattson, In press). In short, more frequent and extensive wildfires potentially accompanying global climate warming will almost certainly reduce short-term opportunities for Yellowstone's grizzly bears to feed on pine seeds, and possibly accelerate the long term loss of this important food.

Global climate warming potentially also interacts with the spread of white pine blister rust to affect future use of pine seeds by Yellowstone's grizzly bears. Blister rust is a non-native fungal pathogen that is highly lethal to whitebark pine (Kendall & Arno, 1990). It is present in whitebark pines in the Yellowstone ecosystem, with the potential to spread more widely (Smith, 1997). Recent research suggests, in fact, that rate of spread will be accelerated by warming (Koteen, 1999) and outpace any other effects of climate change. Consequently, whether increased fire ultimately accelerates the decline of whitebark pine or not, it is likely that much of this important source of food for Yellowstone's grizzly bears will be lost to blister rust. Moreover, reduced use of pine seeds by bears will likely precede outright losses of whitebark pine because cone crops are lost before trees die from infection (Kendall & Arno, 1990) and because use of pine seeds by grizzly bears is sensitive to cone crop size.

The potential effects of climate warming on Yellowstone's elk and bison populations, and thus on Yellowstone's grizzly bears, are unclear. Bison and elk populations in the study area are probably limited by the severity of winters (Meagher, 1973; DelGiudice, Singer & Seal, 1991; DelGiudice *et al.*, 1994; Turner *et al.*, 1994; Kirkpatrick *et al.*, 1996) interacting in complex ways with human harvest strategies. There also is evidence that summer forage affects the size of elk populations (Merrill & Boyce, 1991). If winter severity lessens, then ungulate populations may increase, especially if the extent and quality of summer range increases or remains unchanged. If so, then there may be more ungulates available to bears, although benefits to the different genders would depend on whether the seasonal distribution of ungulate mortality changed or not. If more elk and bison were dying at times other than Spring, then males would probably accrue more of the benefits of population increases. Also, all else equal, increased ungulate populations could result in increased opportunities to

graze thistle, dandelions, and graminoids. However, as discussed above, overall drying could negate this potential.

This information provides a useful basis for anticipating what might happen to grizzly bear diets and reproduction in Yellowstone as the climate warms and blister rust spreads. Use of whitebark pine seeds will almost certainly decline, perhaps to virtually nil. Use of ungulates may increase, but with the potential for that increase disproportionately among males. Among lower-quality foods, grizzly bears will probably be consuming more ants, biscuitroots, and mushrooms, and, with the possible exception of dandelions, consuming less foliage, fewer yampa roots, and fewer pocket gophers or pocket gopher food caches. Commensurate with these changes, cub production likely will decline as a consequence of fewer litters per female consisting more often of 2 rather than 3 cubs. Such a decline might be mitigated by increased cub production caused by greater consumption of ungulates. However, it is even more likely that such increases would be offset by the lower cub survival that accompanies use of proteinaceous foods by reproductive females. It also may be that no increases in cub production would come from increased ungulate populations if males accrued most of the benefits. The reproductive success of Yellowstone's female grizzly bears likely will decline over the next century.

Several researchers have concluded based on analysis of demographic rates that reproduction has little overall effect on the trajectory of bear populations, especially in contrast to the survival of females (Eberhardt *et al.*, 1994; Hovey & McLellan, 1996; Mace & Waller, 1998). Yet, by first principles, birth rates are as important as death rates in determining growth of populations; i.e., growth only occurs if births exceed deaths. Moreover, densities of brown and grizzly bear populations vary by orders-of-magnitude, almost certainly because of differences in the quality and quantity of available foods (Miller *et al.*, 1997; Hilderbrand *et al.*, 1999). Much of these food-related effects on density are speculated to be via female reproductive rate (Stringham, 1990b; Hilderbrand *et al.*, 1999). In contrast to work restricted to vital rates, these latter results suggest that declines in abundance of critical high-quality foods will precipitate declines in life-time reproduction of females with potentially major related declines in bear densities. Reconciling relations between foods and densities with research focused on demography may lie in better understanding methods for decomposing the variance of population growth rate. In

particular, methods of variance decomposition provide snapshots of instantaneous "effects" that vary as vital rates change (Caswell, 1989). Such instantaneous appraisals of growth rate probably do not provide much insight into the consequences of fundamental changes in habitat. There is a good chance that the potential loss of most whitebark pine in the Yellowstone ecosystem and related probable declines in female reproduction will result in declining densities of grizzly bears in the Yellowstone ecosystem.

References

- Adams, C. E. (1972). Aging and reproduction. In *Reproductive patterns. Book 4. Reproduction in mammals*: 128–156. Austin, C. R. & Short, R. V. (Eds.). Cambridge, U. K.: Cambridge Univ. Press.
- Allen, W. V. (1976). Biochemical aspects of lipid storage and utilization in animals. *Amer. Zool.* 16: 631–647.
- Alt, G. L. (1989). *Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania*. Morgantown, W. V.: Ph.D. Dissertation, West Virginia Univ.
- Altmann, J., Hausfater, G. & Altmann, S. A. (1988). Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 325–343. Clutton-Brock, T. H. (Ed.). Chicago, Ill.: Univ. Chicago Press.
- Anderson, D. J. (1982). The home range: a new nonparametric estimation technique. *Ecology* 63: 102–112.
- Andrewartha, H. G. & Birch, L. C. (1954). *The distribution and abundance of animals*. Chicago, Ill.: Univ. Chicago Press.
- Arnould, J. P. Y. & Ramsay, M. A. (1994). Milk production and milk consumption in polar bears during the ice-free period in western Hudson Bay. *Can. J. Zool.* 72: 1365–1370.
- Atkinson, S. N., Nelson, R. A. & Ramsay, M. A. (1996). Changes in the body composition of fasting polar bears (*Ursus maritimus*): the effects of relative fatness on protein conservation. *Phys. Zool.* 69: 304–316.
- Ballard, W. B., Spraker, T. H. & Taylor, K. P. (1981). Causes of neonatal moose calf mortality in south central Alaska. *J. Wildl. Manage.* 45: 335–342.
- Bartlein, P. J., Whitlock, C. & Shafer, S. L. (1997). Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conserv. Biol.* 11: 782–792.
- Barry, T. N. & Blaney, B. J. (1987). Secondary compounds of forages. In *The nutrition of herbivores*: 91–120. Hacker, J. B. & Ternouth, J. H. (Eds.). Sydney, Australia: Academic Press.
- Blanchard, B. M. (1987). Size and growth patterns of the Yellowstone grizzly bear. *Int. Conf. Bear Res. & Manage.* 7: 99–107.

- Blanchard, B. M. & Knight, R. R. (1990). Effects of the 1988 wildfires on Yellowstone grizzly bears. In *Yellowstone grizzly bear investigations: report of the Interagency Study Team 1989*: 13–18. Knight, R. R., Blanchard, B. M. & Mattson, D. J. Bozeman, Mont.: U. S. Dept. Int., Natl. Park Serv.
- Blanchard, B. M. & Knight, R. R. (1991). Movements of Yellowstone grizzly bears. *Biol. Conserv.* 58: 41–67.
- Blanchard, B. M. & Knight, R. R. (1996). Effects of wildfire on grizzly bear movements and food habits. *Int. J. Wildland Fire* 6: 117–122.
- Boertje, R. D., Gasaway, W. C., Grangaard, D. V. & Kelleyhouse, D. G. (1988). Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. *Can. J. Zool.* 66: 2492–2499.
- Boyce, M. S. & Gaillard, J.-M. (1992). Wolves in Yellowstone, Jackson Hole, and the North Fork of the Shoshone River: simulating ungulate consequences of wolf recovery. In *Wolves for Yellowstone? Vol. IV. Research & analysis*: 4.72–4.130. Varley, J. D. & Brewster, W. G. (Eds.). Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Boyd, R. N. (1985). Observations, explanatory power, and simplicity: toward a non-Humean account. In *Observation, experiment and hypothesis in modern physical science*: 47–94. Achinstein, P. & Hannaway, O. (Eds.). Cambridge, Mass.: MIT Press.
- Brian, M. V. (Ed.) (1978). *Production ecology of ants and termites*. Cambridge, U. K.: Cambridge Univ. Press.
- Bunnell, F. L. & Hamilton, T. (1983). Forage digestibility and fitness in grizzly bears. *Int. Conf. Bear Res. & Manage.* 5: 179–185.
- Bunnell, F. L. & Tait, D. E. N. (1981). Population dynamics of bears — implications. In *The dynamics of large mammal populations*: 75–98. Fowler, C. W. & Smith, T. D. (Eds.). New York, N. Y.: John Wiley & Sons.
- Burnham, K. P. & Anderson, D. R. (1998). *Model selection and inference: a practical information-theoretic approach*. New York, N. Y.: Springer.
- Campbell, R. G., Taverner, M. R. & Curic, D. M. (1988). The effects of sex and live weight on the growing pigs response to dietary protein. *Anim. Prod.* 46: 123–130.
- Canfield, J. & Harting, A. L. (1987). Home range and movements. In *Grizzly bear compendium*: 27–33. LeFranc, M. N., Jr., Moss, M. B., Patnode, K. A. & Sugg, W. C., III (Eds.). Denver, Colo.: Interagency Grizzly Bear Committee.

- Case, R. L. & Buckland, L. (1998). Reproductive characteristics of grizzly bears in the Kugluktuk area, Northwest Territories, Canada. *Ursus* 10: 41–47.
- Caswell, H. (1989). *Matrix population models: construction, analysis, and interpretation*. Sunderland, Mass.: Sinauer, Assoc.
- Cattet, M. (1990). Predicting nutritional condition in black bears and polar bears on the basis of morphological and physiological measurements. *Can. J. Zool.* 68: 32–39.
- Chase, J. D., Howard, W. E. & Roseberry, J. T. (1982). Pocket gophers. In *Wild mammals of North America*: 239–255. Chapman, J. A. & Feldhamer, G. A. (Eds.). Baltimore, Maryl.: Johns Hopkins Univ. Press.
- Clark, J. D. & Smith, K. G. (1994). A demographic comparison of two black bear populations in the interior highlands of Arkansas. *Wildl. Soc. Bull.* 22: 593–603.
- Clutton-Brock, T. H. & Harvey, P. H. (1983). The functional significance of variation in body size among mammals. In *Advances in the study of mammalian behavior*: 632–663. Eisenberg, J. F. & Kleiman, D. G. (Eds.). Am. Soc. Mammal. Spec. Publs. 7.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1988). Reproductive success in male and female red deer. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 325–343. Clutton-Brock, T. H. (Ed.). Chicago, Ill.: Univ. Chicago Press.
- Cochran, W. G. (1983). *Planning and analysis of observational studies*. New York, N. Y.: John Wiley & Sons.
- Coenen-Staß, D., Schaarschmidt, B. & Lamprecht, I. (1980). Temperature distribution and calorimetric determination of heat production in the nest of the wood ant, *Formica polyctena* (Hymenoptera, Formicidae). *Ecology* 61: 238–244.
- Cole, G. F. (1969). *The elk of Grand Teton and southern Yellowstone National Parks*. Grand Teton National Park, Wyo.: U.S. National Park Service Res. Rep. GRTE-N-1.
- Collins, W. B., Urness, P. J. & Austin, D. D. (1978). Elk diets and activities on different lodgepole pine habitat segments. *J. Wildl. Manage.* 42: 799–810.
- Crabtree, R. L. & Sheldon, J. W. (1999). Coyotes and canid coexistence in Yellowstone. In *Carnivores in ecosystems: the Yellowstone experience*: 127–163. Clark, T. W., Curlee, A. P., Minta, S. C. & Kareiva, P. M. (Eds.) New Haven, Conn.: Yale Univ. Press.
- Craighead, J. J., Sumner, J. S. & Mitchell, J. A. (1995). *The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959-1992*. Washington, D. C.: Island Press.

- Craighead, L., Paetkau, D., Reynolds, H. V., Vyse, E. R. & Strobeck, C. (1995). Microsatellite analysis of paternity and reproduction in arctic grizzly bears. *J. Heredity* 86: 255–261.
- Cronquist, A. (1994). *Intermountain flora. Vol. 5. Asterales*. Bronx, N. Y.: The New York Botanical Gardens.
- Cunningham, H. M., Friend, D. W. & Nicholson, J. W. G. (1962). Efficiency of conversion of protein, energy, and carbon in pigs restricted late in the fattening period. *Can. J. Anim. Sci.* 42:176–182.
- Darling, L. M. (1987). Habitat use by grizzly bear family groups in interior Alaska. *Int. Conf. Bear Res. & Manage.* 7: 169–178.
- Davies, A. S., Pearson, G. & Carr, J. R. (1986). Effects of feeding level, protein level, and sex of pig on carcass fatness measured by dissection and optical probe methods. *N. Z. J. Exp. Agric.* 14: 301–306.
- Dawid, A. P. (1979). Conditional independence in statistical theory. *J. R. Stat. Soc. B* 41: 1–31.
- Dean, F. C., Darling, L. M. & Lierhaus, A. G. (1986). Observations of intraspecific killing by brown bears, *Ursus arctos*. *Can. Field-Nat.* 100: 208–211.
- DelGiudice, G. D., Singer, F. J. & Seal, U. S. (1991). Physiological assessment of winter nutritional deprivation in elk of Yellowstone National Park. *J. Wildl. Manage.* 55: 653–664.
- DelGiudice, G. D., Rogers, L. L., Allen, A. W. & Seal, U. S. (1991). Weights and hematology of wild black bears during hibernation. *J. Wildl. Diseases* 27: 637–642.
- DelGiudice, G. D., Singer, F. J., Seal, U. S. & Bowser, G. (1994). Physiological responses of Yellowstone bison to winter nutritional deprivation. *J. Wildl. Manage.* 58: 24–34.
- Demaris, A. (1992). *Logit modeling: practical applications*. Newbury Park, Calif.: Sage Publ.
- Derocher, A. E. & Stirling, I. (1995). Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. *Can. J. Zool.* 73: 1657–1665.
- Derocher, A. E. & Stirling, I. (1996). Aspects of survival in juvenile polar bears. *Can. J. Zool.* 74:1246–1252.
- Derocher, A. E., Andriashek, D. & Arnould, J. P. Y. (1993). Aspects of milk composition and lactation in polar bears. *Can. J. Zool.* 71: 561–567.

- Derocher, A. E., Stirling, I. & Andriashek, D. (1992). Pregnancy rates and serum progesterone levels of polar bears in western Hudson Bay. *Can. J. Zool.* 70: 561-566.
- Despain, D. G. (1987). The two climates of Yellowstone National Park. *Proc. Mont. Acad. Sci.* 47: 11-19.
- Despain, D. G. (1990). *Yellowstone's vegetation: the consequences of history and environment in a natural setting*. New York, N. Y.: Robert Rinehart.
- Dirks, R. A. & Martner, B. E. (1982). *The climate of Yellowstone and Grand Teton National Parks*. Washington, D. C.: U.S. Park Serv. Occ. Pap. 6.
- Eagle, T. C. & Pelton, M. R. (1983). Seasonal nutrition of black bears in the Great Smoky Mountains National Park. *Int. Conf. Bear Res. & Manage.* 5: 94-101.
- Eberhardt, L. L. & Knight, R. R. (1996). How many grizzlies in Yellowstone? *J. Wildl. Manage.* 60: 416-421.
- Eberhardt, L. L. & Thomas, J. M. (1991). Designing environmental field studies. *Ecol. Monogr.* 61: 53-73.
- Eberhardt, L. L., Blanchard, B. M. & Knight, R. R. (1994). Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Can. J. Zool.* 72: 360-363.
- Edge, W. D., Marcum, C. L. & Olson-Edge, S. (1987). Summer habitat selection by elk in western Montana: a multivariate approach. *J. Wildl. Manage.* 51: 844-851.
- Edwards, A. W. F. (1972). *Likelihood*. Cambridge, U.K.: Cambridge Univ. Press.
- Eiler, J. H., Wathen, W. G. & Pelton, M. R. (1989). Reproduction in black bears in the southern Appalachian Mountains. *J. Wildl. Manage.* 53: 353-360.
- Egbert, A. L. & Stokes, A. W. (1976). The social behaviour of brown bears on an Alaskan salmon stream. *Int. Conf. Bear Res. & Manage.* 3: 41-56.
- Elgmork, K. & Unander, S. (1998). Brown bear use of ant mounds in Scandinavia. *Ursus* 10: 269-274.
- Elowe, K. D. & Dodge, W. D. (1989). Factors affecting black bear reproductive success and cub survival. *J. Wildl. Manage.* 53: 962-968.
- Ellison, L. & Aldous, C. M. (1952). Influence of pocket gophers on vegetation of subalpine grassland in central Utah. *Ecology* 33: 177-186.

- Erickson, A. W., Mossman, H. W., Hensel, R. J. & Troyer, W. A. (1968). The breeding biology of the male brown bear (*Ursus arctos*). *Zoologica* 53: 85-105.
- Fancy, S. G. & White, R. G. (1985). Incremental cost of activity. In *Bioenergetics of wild herbivores*: 143-159. Hudson, R. J. & White, R. G. (Eds.). Boca Raton, Flor.: CRC Press.
- Farley, S. D. & Robbins, C. T. (1994). Development of two methods to estimate body composition of bears. *Can. J. Zool.* 72: 220-226.
- Farley, S. D. & Robbins, C. T. (1995). Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* 73:2216-2222.
- Farnes, P., Heydon, C. & Hansen, K. (1999). *Snowpack distribution in Grand Teton National Park and the Snake River drainage above Jackson, Wyoming*. Bozeman, Mont.: Final Rep., Coop. Agreement No. CA 1268-1-9017, Contract No. 291791.
- Findley, J. S. (1951). Habitat preference of four species of *Microtus* in Jackson Hole, Wyoming. *J. Mammal.* 32: 118-120.
- Fischer, W. C. (1981). *Photo guide for appraising downed woody fuels in Montana forests: lodgepole pine, and Engelmann spruce-subalpine fir cover types*. U. S. For. Serv. Gen. Tech. Rep. INT-98.
- Fisher, R. A. (1960). *The design of experiments*. New York, N. Y.: Hafner Publ. Co.
- Frank, D. A. & McNaughton, S. J. (1993). Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* 96: 157-161.
- French, S. P. & French, M. G. (1990). Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986-88. *Int. Conf. Bear Res. & Manage.* 8: 335-442.
- French, S. P., French, M. G. & Knight, R. R. (1994). Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *Int. Conf. Bear Res. & Manage.* 9: 389-400.
- Freer, M. (1981). The control of food intake by grazing animals. In *Grazing animals*: 105-124. Morley, F. H. W. (Ed.). Amsterdam, Netherl.: Elsevier Sci. Publ. Co.
- Frisch, R. E. (1990). Body fat, menarche, fitness and fertility. In *Adipose tissue and reproduction*: 1-26. Frisch, R. E. (Ed.). Basel, Switz.: Karger.
- Fryxell, J. M. & Sinclair, A. R. E. (2000). A dynamic view of population regulation. In *Ecology and management of large mammals in North America*: 156-174. Demarais, S. & Krausman, P. R. (Eds.). Upper Saddle River, N. J.: Prentice Hall.

- Garland, T., Jr. (1983). Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* 121: 571–587.
- Garton, E. O., Crabtree, R. L., Ackerman, B. B. & Wright, G. (1992). Potential impacts of Yellowstone wolves on Clarks Fork elk herd. In *Wolves for Yellowstone? Vol. IV. Research & analysis*: 4.131–4.146. Varley, J. D. & Brewster, W. G. (Eds.). Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Gaud, W. S., Balda, R. P. & Brawn, J. D. (1986). The dilemma of plots or years: a case for long-term studies. In *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*: 223–227. Verner, J., Morrison, M. L. & Ralph, C. J. (Eds.). Madison, Wisc.: Univ. Wisconsin Press.
- Gautestad, A. O. & Mysterud, I. (1993). Physical and biological mechanisms in animal movement processes. *J. Appl. Ecol.* 30: 523–535.
- Gautestad, A. O. & Mysterud, I. (1995). The home range ghost. *Oikos* 74: 195–204.
- Gautestad, A. O., Mysterud, I. & Pelton, M. R. (1998). Complex movement and scale-free habitat use: testing the multi-scale home-range model on black bear telemetry data. *Ursus* 10: 219–234.
- Gilbert, B. K. (1999). Opportunities for social learning in bears. *Symp. Zool. Soc. Lond.* 73: In press.
- Gilbert, B. K. & Lanner, R. M. (1995). Energy, diet selection and restoration of brown bear populations. Grenoble, France: *European session — Int. Conf. Bear Res. & Manage* 9: 231–240.
- 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.: M. S. Thesis, Mont. State Univ.
- Green, G. I., Mattson, D. J. & Peek, J. M. (1997). Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *J. Wildl. Manage* 61: 1040–1055.
- Green, R. H. (1979). *Sampling design and statistical methods for environmental biologists*. New York, N. Y.: John Wiley & Sons.
- Gregg, R. E. (1963). *The ants of Colorado*. Boulder, Colo.: Univ. Colo. Press.
- Gross, J. E., Wang, Z. & Wunder, B. A. (1985). Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. *J. Mammal.* 66: 661–667.

- Gross, J. E., Shipley, L. A., Hobbs, N. T., Spalinger, D. E. & Wunder, B. A. (1993). Functional response of herbivores in food-concentrated patches: test of a mechanistic model. *Ecology* 74: 778–791.
- Gunther, K. A. & Renkin, R. A. (1990). Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. *Int. Conf. Bear Res. & Manage.* 8: 329–334.
- Haley, M. P., Deutsch, C. J. & LeBoeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim. Behav.* 48: 1249–1260.
- Hamer, D. & Herrero, S. (1987). Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. *Int. Conf. Bear Res. & Manage.* 7: 199–214.
- Hamer, D. & Herrero, S. (1990). Courtship and use of mating areas by grizzly bears in the Front Ranges of Banff National Park, Alberta. *Can. J. Zool.* 68: 2695–2697.
- Hansen, J. E., Sato, M., Ruedy, R., Lacis, A. & Glascoe, J. (1998). Global climate data and models: a reconciliation. *Science* 281: 930–932.
- Hansteen, T. L., Andreassen, H. P. & Ims, R. A. (1997). Effects of spatiotemporal scale on autocorrelation and home range estimators. *J. Wildl. Manage.* 61: 280–290.
- Harestad, A. S. & Bunnell, F. L. (1979). Home range and body weight – a reevaluation. *Ecology* 60: 389–402.
- Haroldson, M. & Mattson, D. J. (1985). *Responses of grizzly bears to backcountry human use in Yellowstone National Park*. Bozeman, Mont.: U. S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Harting, A. L. (1985). *Relationships between activity patterns and foraging strategies of Yellowstone grizzly bears*. Bozeman, Mont.: M. S. Thesis, Mont. State Univ.
- Harvey, P. H. & Harcourt, A. H. (1984). Sperm competition, testes size, and breeding systems in primates. In *Sperm competition and the evolution of mating systems*: 589–600. Smith, R. L. (Ed.). Orlando, Flor.: Academic Press.
- Harvey, P. H. & Zammuto, R. M. (1985). Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature* 315: 319–320.
- Hellgren, E. C. (1998). Physiology of hibernation in bears. *Ursus* 10: 467–478.
- Herrero, S. (1978). A comparison of some features of the evolution, ecology and behavior of black and grizzly/brown bears. *Carnivore* 1: 7–17.

- Herrero, S. (1985). *Bear attacks: their causes and avoidance*. New York, N. Y.: Nick Lyons Books.
- Hilborn, R. & Mangel, M. (1997). *The ecological detective: confronting models with data*. Princeton, N. J.: Princeton Univ. Press.
- Hildebrand, G. V., Schwartz, C. C., Robbins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M. & Servheen, C. (1999). Importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* 77: 132–138.
- Hillel, D. (1980). *Fundamentals of soil physics*. New York, N. Y.: Academic Press.
- Hodgson, J. R. (1970). *Ecological distribution of Microtus montanus (Peale) and Microtus pennsylvanicus (Ord) in an area of geographic sympatry in southwestern Montana*. Bozeman, Mont.: Ph. D. Dissertation, Mont. State Univ.
- Hodgson, J. (1986). Grazing behaviour and herbage intake. In *Grazing: occasional symposium no. 19, British Grassland Society*: 51–64. Frame, J. (Ed.). Lavenham, Suffolk, U.K.: Lavenham Press Ltd.
- Holcroft, A. C. & Hererro, S. (1984). Grizzly bear digging sites for *Hedysarum sulpherescens* roots in southwestern Alberta. *Can. J. Zool.* 62: 2571–2575.
- Holland, P. W. (1986). Statistics and causal inference. *J. Am. Stat. Assoc.* 81:945–960.
- Houston, D. B. (1978). Elk as winter-spring food for carnivores in northern Yellowstone Park. *J. Appl. Ecol.* 15: 653–661.
- Houston, D. B. (1982). *The northern Yellowstone elk*. New York, N. Y.: Macmillan Publ. Co.
- Hovey, F. W. & McLellan, B. N. (1996). Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Can. J. Zool.* 74: 1409–1416.
- Hutchins, H. E. & Lanner, R. M. (1982). The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* 55: 192–201.
- Ingles, L. G. (1952). The ecology of the mountain pocket gopher, *Thomomys monticola*. *Ecology* 33: 87–95.
- Jacoby, M. E., Hilderbrand, G. V., Servheen, C., Schwartz, C. C., Arthur, S. M., Hanley, T. A., Robbins, C. T. & Michener, R. (1999). Trophic relations of brown and black bears in several western North American ecosystems. *J. Wildl. Manage.* 63: 921–929.

- Jenness, R., Erickson, A. W. & Craighead, J. J. (1972). Some comparative aspects of milk from four species of bears. *J. Mammal.* 53: 34–47.
- Johnson, D. H. (1980). The comparison of usage and availability measurement for evaluating resource preference. *Ecology* 61: 65–71.
- Johnson, D.H. (1999). The insignificance of statistical significance testing. *J. Wildl. Manage.* 63: 763–772.
- Johnson, R. A. & Wichern, D. W. (1992). *Applied multivariate statistical analysis*. (3rd edn.). Englewood Cliffs, N. J.: Prentice Hall.
- Jonkel, C. & Cowan, I. McT. (1971). The black bear in the spruce-fir forest. *Wildl. Monogr.* 27:1–57.
- Karasov, W. H. & Diamond, J. M. (1988). Interplay between physiology and ecology in digestion. *BioScience* 38: 602–611.
- Keane, R. E., Arno, S. F., Brown, J. K. & Tomback, D. F. (1990). Modelling stand dynamics in whitebark pine (*Pinus albicaulis*) forests. *Ecol. Modelling* 51: 73–95.
- Keane, R. E., Ryan, K. C. & Running, S. W. (1996). Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. *Tree Phys.* 16: 319–332.
- Kendall, K. C. (1983). Use of pine nuts by black and grizzly bears in the Yellowstone area. *Int. Conf. Bear Res. & Manage.* 5: 166–173.
- Kendall, K. C. & Arno, S. F. (1990). Whitebark pine – an important but endangered wildlife resource. In *Proceedings — whitebark pine ecosystems: ecology and management of a high-mountain resource*: 264–273. Schmidt, W. C. & McDonald, K. J. (Compilers). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-270.
- Kendall, P. T. (1984). The use of fat in dog and cat diets. In *Fats in animal nutrition*: 383–404. Wiseman, J. (Ed.). London: Butterworths.
- Kerr, R. A. (1998). Among global thermometers, warming still wins out. *Science* 281: 1948–1949.
- Kidd, M. G. & Longair, R. W. (1997). Abundance and diversity of ant (Hymenoptera: Formicidae) assemblages in regenerating forests of northern Saskatchewan. *Can. Field-Natur.* 111: 635–637.
- Kie, J. G., Baldwin, J. A. & Evans, C. J. (1994). *CALHOME home range analysis program electronic user's manual*. Fresno, Calif.: U. S. Forest Service, Pacific Southwest Res. Sta.

- Kingsley, M. C. S., Nagy, J. A. & Reynolds, H. V. (1988). Growth in length and weight of northern brown bears: differences between sexes and populations. *Can. J. Zool.* 66: 981–986.
- Kirkpatrick, J. F., McCarthy, J. C., Gudermuth, D. F., Shideler, S. E. & Lasley, B. L. (1996). An assessment of the reproductive biology of Yellowstone bison (*Bison bison*) subpopulations using noncapture methods. *Can. J. Zool.* 74: 8–14.
- Klinkhamer, P. G. L. & De Jong, T. J. (1993). Biological flora of the British Isles. 176. *Cirsium vulgare* (Savi) Ten. *J. Ecology* 81: 177–191.
- Knight, R. R. & Eberhardt, L. L. (1985). Population dynamics of Yellowstone grizzly bears. *Ecology* 66: 323–334.
- Knight, R. R., Blanchard, B. M. & Kendall, K. C. (1982). *Yellowstone grizzly bear investigations: annual report of the Interagency Study Team 1981*. Bozeman, Mont.: U.S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Knight, R. R., Blanchard, B. M. & Mattson, D. J. (1993). *Yellowstone grizzly bear investigations: annual report of the Interagency Study Team 1992*. Bozeman, Mont.: U.S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Knight, R. R., Blanchard, B. M., Kendall, K. C. & Oldenburg, L. E. (1980). *Yellowstone grizzly bear investigations: annual report of the Interagency Study Team 1978 and 1979*. Bozeman, Mont.: U.S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Knight, R., Basile, J., Greer, K., Judd, S., Oldenburg, L. & Roop, L. (1977). *Yellowstone grizzly bear investigations: annual report of the Interagency Study Team 1976*. Bozeman, Mont.: U.S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Knight, R., Basile, J., Greer, K., Judd, S., Oldenburg, L. & Roop, L. (1978). *Yellowstone grizzly bear investigations: annual report of the Interagency Study Team 1977*. Bozeman, Mont.: U.S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Kolenosky, G. B. (1990). Reproductive biology of black bears in east-central Ontario. *Int. Conf. Bear Res. & Manage.* 8: 385–392.
- Koteen, L. (1999). *Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone ecosystem*. New Haven, Conn.: M. S. Thesis, Yale Univ.
- Krebs, C. J. (1995). Two paradigms of population regulation. *Wildl. Res.* 22: 1–10.
- Kyburg, H. E. (1969). *Probability theory*. Englewood Cliffs, N. J.: Prentice-Hall.
- Langbein, L. I. & Lichtman, A. J. (1978). *Ecological inference*. Beverley Hills, Calif.: Sage Publ.

- Lanner, R. M. & Gilbert, B. K. (1994). Nutritive value of whitebark pine seeds, and the question of their variable dormancy. In *Proceedings — international workshop on subalpine stone pines and their environment: the status of our knowledge*: 206–211. Schmidt, W. C. & Holtmeier, F.-K. (Eds.). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-GTR-309.
- Laudan, L. (1977). *Progress and its problems: towards a theory of scientific growth*. Berkeley, Calif.: Univ. Calif. Press.
- Laycock, W. A. & Richardson, B. Z. (1975). Long-term effects of pocket gopher control on vegetation and soils of a subalpine grassland. *J. Range Manage.* 28: 458–462.
- Leberg, P. L., Brisbin, I. L., Jr., Smith, M. H & White, G. C. (1989). Factors affecting the analysis of growth patterns of large mammals. *J. Mamm.* 70: 275–283.
- LeCount, A. L. (1982). Characteristics of a central Arizona black bear population. *J. Wildl. Manage.* 46: 861–868.
- Long, B., Hinschberger, M., Roby, G. & Kimbal, J. (1980). *Gros Ventre cooperative elk study: final report 1974–1979*. Jackson, Wyo.: Wyoming Game & Fish Dept. and Bridger-Teton National Forest.
- Mace, R. D. & Waller, J. S. (1997). Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *J. Wildl. Manage.* 61: 39–52.
- Mace, R. D. & Waller, J. S. (1998). Demography and population trend of grizzly bears in the Swan Mountains, Montana. *Conserv. Biol.* 12: 1005–1016.
- Mack, J. A. & Singer, F. J. (1992). Predicted effects of wolf predation on Northern Range elk, mule deer, and moose using POP-II models. In *Wolves for Yellowstone? Vol. IV. Research & analysis*: 4.43–4.70. Varley, J. D. & Brewster, W. G. (Eds.). Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Mack, J. A., Singer, F. J. & Messaros, M. E. (1990). The ungulate prey base for wolves in Yellowstone National Park; II. In *Wolves for Yellowstone? Vol. II. Research & analysis*: 2.40–2.235. Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Manning, J. T. (1985). Choosy females and correlates of male age. *J. Theor. Biol.* 116: 349–354.
- Marcum, C. L. & Scott, M. D. (1985). Influences of weather on elk use of spring-summer habitat. *J. Wildl. Manage.* 49: 73–76.
- Mattson, D. J. (1984). *Classification and environmental relationships of wetland vegetation in central Yellowstone National Park*. Moscow, Id.: M. S. Thesis, Univ. of Idaho.

- Mattson, D. J. (1990). Human impacts on bear habitat use. *Int. Conf. Bear Res. & Manage.* 8: 33–56.
- Mattson, D. J. (1991). *Field manual for the collection of grizzly bear habitat data in the Yellowstone ecosystem: 1991 revision*. Bozeman, Mont.: U.S. Natl. Park Serv., Interagency Grizzly Bear Study Team.
- Mattson, D. J. (1997a). Use of lodgepole pine cover types by Yellowstone grizzly bears. *J. Wildl. Manage.* 61: 480–496.
- Mattson, D. J. (1997b). Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biol. Conserv.* 81: 161–177.
- Mattson, D. J. (1997c). Selection of microsites by grizzly bears to excavate biscuitroots. *J. Mammal.* 78: 228–238.
- Mattson, D. J. (1998). Diet and morphology of extant and recently extinct northern bears. *Ursus* 10: 479–496.
- Mattson, D. J. & Reinhart, D. P. (1990). Whitebark pine on the Mount Washburn massif, Yellowstone National Park. In *Proceedings – symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*: 106–117. In Schmidt, W. C. & McDonald, K. J. (Compilers). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-270.
- Mattson, D. J. & Reinhart, D. P. (1994). Bear use of whitebark pine seeds in North America. In *Proceedings – international workshop on subalpine stone pines and their environment: the status of our knowledge*: 212–220. Schmidt, W. C. & Holtmeier, F.-K. (Eds.). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-GTR-309.
- Mattson, D. J. & Reinhart, D. P. (1995). Influences of cutthroat trout (*Onchorynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. *Can. J. Zool.* 73: 2072–2079.
- Mattson, D. J. & Reinhart, D. P. (1997). Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *J. Appl. Ecol.* 34: 926–940.
- Mattson, D. J., Blanchard, B. M. & Knight, R. R. (1991a). Food habits of Yellowstone grizzly bears, 1977–87. *Can. J. Zool.* 69: 1619–1629.
- Mattson, D. J., Blanchard, B. M. & Knight, R. R. (1992a). Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *J. Wildl. Manage.* 56: 432–442.

- Mattson, D. J., Kendall, K. C. & Reinhart, D. P. (In press). Whitebark pine, grizzly bears, and red squirrels. In *Whitebark pine communities: ecology and restoration*: 000–000. Tomback, D. F., Arno, S. F. & Keane, R. E. (Eds.). Washington, D. C.: Island Press.
- Mattson, D. J., Knight, R. R. & Blanchard, B. M. (1987). The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Int. Conf. Bear Res. & Manage.* 7: 259–273.
- Mattson, D. J., Knight, R. R. & Blanchard, B. M. (1992b). Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975–1990. *J. Mammal.* 73: 422–425.
- Mattson, D. J., Reinhart, D. P. & Blanchard, B. M. (1994). Variation in production and use of whitebark pine seeds in the Yellowstone area. In *Plants and their environment: proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem*: 205–220. Despain, D. G. (Ed.). U. S. Natl. Park Serv. Tech. Rep. NPS/NRYELL/NRTR.
- Mattson, D. J., Barber, K., Maw, R. & Renkin, R. (1999). *Coefficients of productivity for Yellowstone's grizzly bear habitat*. Moscow, Id.: U. S. G. S. Forest & Rangeland Ecosys. Sci. Cen.
- Mattson, D. J., Gillin, C. M., Benson, S. A. & Knight, R. R. (1991b). Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Can. J. Zool.* 69: 2430–2435.
- Mattson, D. J., Wright, R. G., Kendall, K. C. & Martinka, C. J. (1995). Grizzly bears. In *Our living resources*: 103–105. LaRoe, E. T., Farris, G. S., Puckett, C. E., Doran, P. D. & Mac, M. J. (Eds.). Washington, D. C.: U. S. Dept. Int. Natl. Biol. Serv.
- McCann, R. K. (1998). *Kluane National Park grizzly bear research project: draft final report*. Vancouver, B. C.: Centre for Appl. Conserv. Biol., Univ. British Columbia.
- McDonald, P., Edwards, R. A. & Greenhalgh, J. F. D. (1988). *Animal nutrition*. (4th edn). New York, N. Y.: Longman Scientific & Technical.
- McLaughlin, C. R., Matula, G. J., Jr. & O'Connor, R. J. (1994). Synchronous reproduction by Maine black bears. *Int. Conf. Bear Res. & Manage.* 9: 471–479.
- McLean, P. K. & Pelton, M. R. (1994). Estimates of population density and growth of black bears in the Smoky Mountains. *Int. Conf. Bear Res. & Manage.* 9: 253–262.
- McLellan, B. (1994). Density-dependent regulation of brown bears. In *Density-dependent population regulation of black, brown, and polar bears*: 15–24. Taylor, M. (Ed.). *Int. Conf. Bear Res. & Manage Monogr.* 3.

- McLellan, B. N. & Shackleton, D. M. (1988). Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. *J. Appl. Ecol.* 25: 451-460.
- Meagher, M. M. (1973). *The bison of Yellowstone National Park*. Washington, D. C.: U.S. Natl. Park Serv. Monogr. Series No. 1.
- Meagher, M. (1976). Winter weather as a population regulating influence on free-ranging bison in Yellowstone National Park. In *Symposium on research in national parks*: 29-38. Philadelphia, Penn.: Amer. Assoc. Adv. of Sci.
- Meagher, M. & Fowler, S. (1989). The consequence of protecting problem grizzly bears. In *Bear-people conflicts - proceedings of a conference on management strategies*: 141-144. M. Bromley (Ed.). Yellowknife, N. W. T.: Northwest Terr. Dept. Renew. Res.
- Mealey, S. P. (1980). The natural food habits of grizzly bears in Yellowstone National Park, 1973-74. *Int. Conf. Bear Res. & Manage.* 3: 281-292.
- Merrill, E. H., Boyce, M. S. (1991). Summer range and elk population dynamics in Yellowstone National Park. In *The Greater Yellowstone ecosystem: redefining America's wilderness heritage*: 263-273. Keiter, R. B. & Boyce, M. S. (Eds.). New Haven, Conn.: Yale Univ. Press.
- Merrill, E. H., Bramble-Brodahl, M. K., Marris, R. W. & Boyce, M. S. (1993). Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. *J. Range. Manage.* 46: 151-157.
- Miller, S. D. (1994). Black bear reproduction and cub survivorship in south-central Alaska. *Int. Conf. Bear Res. & Manage.* 9: 263-273.
- Miller, S. D., White, G. C., Sellers, R. A., Reynolds, H. V., Schoen, J. W., Titus, K., Barnes, V. G., Jr., Smith, R. B., Nelson, R. R., Ballard, W. B. & Schwartz, C. C. (1997). Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. *Wildl. Monogr.* 133: 1-55.
- Modig, A. O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Anim. Behav.* 51: 1295-1306.
- Morgan, P. & Bunting, S. C. (1992). Using cone scars to estimate cone crops of whitebark pine. *West. J. Appl. For.* 7: 71-73.
- Mueggler, W. F. & Stewart, W. L. (1980). *Grassland and shrubland habitat types of western Montana*. Ogden, Ut.: U.S. For. Serv. Gen. Tech. Rep. INT-66.
- Murie, A. (1981). *The grizzlies of Mount McKinley*. Washington, D. C.: U. S. Natl. Park Serv. Sci. Monogr. Ser. 14.

- Nagy, J. A. S. & Haroldson, M. A. (1990). Comparisons of some home range and population parameters among four bear populations in Canada. *Int. Conf. Bear Res. & Manage.* 8: 227-236.
- Nelson, R. A. Folk, G. E., Jr., Pfeiffer, E. W., Craighead, J. J., Jonkel, C. J. & Steiger, D. L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Int. Conf. Bear Res. & Manage.* 5: 284-290.
- Noyce, K. V. & Garshelis, D. L. (1994). Body size and blood characteristics as indicators of condition and reproductive performance in black bears. *Int. Conf. Bear Res. & Manage.* 9: 481-496.
- Noyce, K. V., Kannowski, P. B. & Riggs, M. R. (1997). Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. *Can. J. Zool.* 75: 1671-1686.
- O'Brien, S. L. & Lindzey, F. G. (1998). Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. *Ursus* 10: 427-435.
- Oftedal, O. T., Alt, G. L., Widdowson, E. M. & Jakubasz, M. R. (1993). Nutrition and growth of suckling black bears (*Ursus americanus*) during their mother's winter fast. *Brit. J. Nutr.* 70: 59-79.
- Oosterveld, P. (1983). *Taraxacum* species as environmental indicators for grassland management. *Envir. Monitoring & Assessment* 3: 381-389.
- Parker, G. A. (1984). Sperm competition and the evolution of animals mating strategies. In *Sperm competition and the evolution of animal mating systems*: 1-60. Smith, R. L. (Ed.). Orlando, Flor.: Academic Press.
- Pearson, A. M. (1975). *The northern interior grizzly bear Ursus arctos L.* Ottawa: Can. Wildl. Serv. Rep. Ser. 34.
- Pease, C. M. & Mattson, D. J. (1999). Demography of the Yellowstone grizzly bears. *Ecology* 80: 957-975.
- Pekas, J. C. (1991). Digestion and absorption capacity and their development. In *Swine nutrition*: 37-73. Miller, E. R., Ullrey, D. E. & Lewis, A. J. (Eds.). Boston, Mass.: Butterworth-Heinemann.
- Pettigrew, J. E. & Moser, R. L. (1991). Fat in swine nutrition. In *Swine nutrition*: 133-145. Miller, E. R., Ullrey, D. E. & Lewis, A. J. (Eds.). Boston, Mass.: Butterworth-Heinemann.

- Podrutzny, S. R., Reinhart, D. P. & Mattson, D. J. (In press). Fire, red squirrels, whitebark pine and Yellowstone grizzly bears. *Ursus* 11: 000-000.
- Pond, C. M. (1984). Physiological and ecological importance of energy storage in the evolution of lactation: evidence for a common pattern of anatomical organization. *Symp. Zool. Soc. Lond.* 51: 1-32.
- Pond, C. M., Mattacks, C. A., Thompson, M. C. & Sadler, D. (1986). The effects of age, dietary restriction, exercise and maternity on the abundance and volume of adipocytes in twelve adipose depots of adult guinea-pigs. *Brit. J. Nutr.* 56: 29-48.
- Pond, C. M., Mattacks, C. A., Colby, R. H. & Ramsay, M. A. (1992). The anatomy, chemical composition, and metabolism of adipose tissue in wild polar bears (*Ursus maritimus*). *Can. J. Zool.* 70: 326-341.
- Pritchard, G. T. & Robbins, C. T. (1989). Digestive and metabolic efficiencies of grizzly and black bears. *Can. J. Zool.* 68: 1645-1651.
- Prosky, L., Asp, N.-G., Furda, I., Devries, J. W., Schweizer, T. F. & Harland, B. F. (1984). Determination of total dietary fiber in foods, food products, and total diets: interlaboratory study. *J. Assoc. Off. Anal. Chem.* 67: 1044-1052.
- Putnam, H. (1995). *Pragmatism: an open question*. Oxford, U.K.: Blackwell.
- Ramsay, M. A. & Dunbrack, R. L. (1986). Physiological constraints on life history phenomena: the example of small bear cubs at birth. *Am. Nat.* 127: 735-743.
- Ramsay, M. A. & Stirling, I. (1986). On the mating system of polar bears. *Can. J. Zool.* 64: 2142-2151.
- Ramsay, M. A. & Stirling, I. (1988). Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *J. Zool. (Lond.)* 214: 601-634.
- Ramsay, M. A., Mattacks, C. A. & Pond, C. M. (1992). Seasonal and sex differences in the structure and chemical composition of adipose tissue in wild polar bears (*Ursus maritimus*). *J. Zool. (Lond.)* 228: 533-544.
- Reinhart, D. P. & Mattson, D. J. (1990a). Bear use of cutthroat trout spawning streams in Yellowstone National Park. *Int. Conf. Bear Res. & Manage.* 8: 343-350.
- Reinhart, D. P. & Mattson, D. J. (1990b). Red squirrels in the whitebark pine zone. In *Proceedings - symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*: 256-263. In Schmidt, W. C. & McDonald, K. J. (Compilers). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-270.

- Reynolds, H. V., III & Garner, G. W. (1987). Patterns of grizzly predation on caribou in northern Alaska. *Int. Conf. Bear Res. & Manage.* 7:59-67.
- Rogers, L. (1976). Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 41: 431-438.
- Rogers, L. L. (1987). Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildl. Monogr.* 97: 1-72.
- Romme, W. H. & Turner, M. G. (1991). Implications of global climate change for biogeographic patterns in the Greater Yellowstone ecosystem. *Conserv. Biol.* 5: 373-386.
- Rosenbaum, P. R. (1984). From association to causation in observational studies: the role of tests of strongly ignorable treatment assignment. *J. Am. Stat. Assoc.* 79: 41-48.
- Russell, R. H., Nolan, J. W., Woody, N. G. & Anderson, G. H. (1979). *A study of the grizzly bear (Ursus arctos L.) in Jasper National Park, 1975-1978.* Edmonton, Alberta: Can. Wildl. Serv.
- Salmon, W. C. (1970). *Statistical explanation and statistical relevance.* Pittsburg, Penn.: Univ. Pittsburgh Press.
- Salmon, W. C. (1984). *Scientific explanation and the causal structure of the world.* Princeton, N. J.: Princeton Univ. Press.
- Samson, C. & Huot, J. (1995). Reproductive biology of female black bears in relation to body mass in early winter. *J. Mammal.* 76: 68-77.
- Samuel, M. D., Pierce, D. J. & Garton, E. O. (1985). Identifying areas of concentrated use within the home range. *J. Anim. Ecol.* 54: 711-719.
- Sanders, C. J. (1964). The biology of carpenter ants in New Brunswick. *Can. Entomol.* 96: 894-909.
- Sanders, C. J. (1970). The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. *Ecology* 51: 865-873.
- Sanders, C. J. (1972). Seasonal and daily activity patterns of carpenter ants (*Camponotus* spp.) in northwestern Ontario (Hymenoptera: Formicidae). *Can. Entomol.* 104: 1681-1687.
- Schemmel, R. (1976). Physiological considerations of lipid storage and utilization. *Am. Zool.* 16: 661-670.

- Schenk, A. & Kovacs, K. M. (1995). Multiple mating between black bears revealed by DNA fingerprinting. *Anim. Behav.* 50: 1483-1490.
- Scherba, G. (1961). Nest structure and reproduction in the mound-building ant *Formica opaciventris* Emery in Wyoming. *J. New York Ent. Soc.* 64: 71-87.
- 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.: M. S. Thesis, Mont. State Univ.
- Schleyer, B., Jonkel, J., Rhoades, K. & Dunbar, D. (1984). *The effects of nonmotorized recreation on grizzly bear behavior and habitat use.* Bozeman, Mont.: U. S. Natl. Park Serv. Interagency Grizzly Bear Study Team.
- Schwartz, C. C. & Franzmann, A. W. (1991). Interrelationships of black bears to moose and forest succession in the northern coniferous forest. *Wildl. Monogr.* 113.
- Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimators. *J. Wildl. Manage.* 63: 739-747.
- Servheen, C. W. & Knight, R. R. (1990). Possible effects of a restored wolf population on grizzly bears in the Yellowstone area. In *Wolves for Yellowstone? Vol. II. Research & analysis*: 4.35-4.49. Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Seller, R. A. & Aumiller, L. D. (1994). Brown bear population characteristics at McNeil River, Alaska. *Int. Conf. Bear Res. & Manage.* 9: 283-293.
- Shrader-Frechette, K. S. & McCoy, E. D. (1993). *Method in ecology: strategies for conservation.* Cambridge, U.K.: Cambridge Univ. Press.
- Siebrits, F. K., Kemm, E. H., Ras, M. N. & Barnes, P. M. (1986). Protein composition in pigs influenced by sex, type and livemass. 1. The pattern and composition of protein deposition. *S. Afr. J. Anim. Sci.* 16:23-27.
- Singer, F. J. (1990). Some predictions concerning a wolf recovery into Yellowstone National Park. In *Wolves for Yellowstone? Vol. II. Research & analysis*: 4.3-4.34. Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Singer, F. J. (1991). The ungulate prey base for wolves in Yellowstone National Park. In *The greater Yellowstone ecosystem: redefining America's wilderness heritage*: 323-348. Keiter, R. B. & Boyce, M. S. (Eds.). New Haven, Conn.: Yale Univ. Press.
- Singer, F. J. (1995). Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. *Northwest Sci.* 69: 191-203.

- Singer, F. J. & Harter, M. K. (1996). Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. *Ecol. Appl.* 6: 185-199.
- Singer, F. J., Harting, A., Symonds, K. K. & Coughenour, M. B. (1997). Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildl. Manage.* 61: 12-25.
- Smith, D. W., Brewster, W. G. & Bangs, E. E. (1999). Wolves in the Greater Yellowstone Ecosystem: restoration of a top carnivore in a complex management environment. In *Carnivores in ecosystems: the Yellowstone experience*: 103-125. Clark, T. W., Curlee, A. P., Minta, S. C. & Kareiva, P. M. (Eds.) New Haven, Conn.: Yale Univ. Press.
- Smith, J. P. (1997). *Insect and disease problems in Intermountain West whitebark pines with emphasis on white pine blister rust disease*. Moscow, Id.: M. S. Thesis, Univ. of Idaho.
- Smuts, B. B. & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Study Behav.* 22: 1-63.
- Steele, R., Cooper, S. V., Ondov, D. M., Roberts, D. W. & Pfister, R. D. (1983). *Forest habitat types of eastern Idaho-western Wyoming*. Ogden, Ut.: U.S. For. Serv. Gen. Tech. Rep. INT-144.
- Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory*. Princeton, N. J.: Princeton Univ. Press.
- Steuter, A. A., Steinauer, E. M., Hill, G. L., Bowers, P. A. & Tieszen, L. L. (1995). Distribution and diet of bison and pocket gophers in a sandhills prairie. *Ecol. Appl.* 5: 756-766.
- Stonorov, D. & Stokes, A. W. (1972). Social behavior of the Alaskan brown bear. *Int. Conf. Bear Res. & Manage.* 2: 232-241.
- Stirling, I. & Derocher, A. E. (1990). Factor affecting the evolution and behavioral ecology of the modern bears. *Int. Conf. Bear Res. & Manage.* 8: 189-204.
- Stringham, S. F. (1980). Possible impacts of hunting on the grizzly/brown bear, a threatened species. *Int. Conf. Bear Res. & Manage.* 3: 337-349.
- Stringham, S. F. (1983). Roles of adult males in grizzly bear population biology. *Int. Conf. Bear Res. & Manage.* 5: 140-151.
- Stringham, S. F. (1986). Effects of climate, dump closure, and others factors on Yellowstone grizzly bear litter size. *Int. Conf. Bear Res. & Manage.* 6: 33-39.

- Stringham, S. F. (1990a). Black bear reproductive rate relative to body weight in hunted populations. *Int. Conf. Bear Res. & Manage.* 8: 425–432.
- Stringham, S. F. (1990b). Grizzly bear reproductive rate relative to body size. *Int. Conf. Bear Res. & Manage.* 8: 433–443.
- Stubbendieck, J., Hatch, S. L. & Kjar, K. J. (1982). *North American range plants*. (2nd edn). Lincoln, Nebr.: Univ. of Nebr. Press.
- Swenson, J. E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. (1997). Infanticide caused by hunting of male bears. *Nature* 386: 450–451.
- Swihart, R. K. & Slade, N. A. (1985). Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49: 1019–1025.
- Tait, D. E. N. (1980). Abandonment as a reproductive tactic — the example of grizzly bears. *Am. Nat.* 115: 800–808.
- Taylor, M., Larsen, T. & Schweinsberg, R. E. (1985). Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). *Arctic* 38: 303–309.
- Thorne, E. T., Dean, R. E. & Hepworth, W. G. (1976). Nutrition during gestation in relation to successful reproduction in elk. *J. Wildl. Manage.* 40: 330–335.
- Torgersen, T. R. & Bull, E. L. (1995). Down logs as habitat for forest-dwelling ants — the primary prey of pileated woodpeckers in northeastern Oregon. *Northwest Sci.* 69: 294–303.
- Tsubota, T. & Kanagawa, H. (1989). Annual changes in serum testosterone levels and spermatogenesis in the Hokkaido brown bear, *Ursus arctos yesoensis*. *J. Mammal. Soc. Japan* 14: 11–17.
- Tsubota, T., Kanagawa, H., Mano, T. & Aoi, T. (1990). Corpora albicantia and placental scars in Hokkaido brown bear. *Int. Conf. Bear Res. & Manage.* 8: 125–128.
- Turner, G. T., Hansen, R. M., Reid, V. H., Tietjen, H. P. & Ward, A. L. (1973). *Pocket gophers and Colorado mountain rangeland*. Fort Collins, Colo.: Colo. State Univ. Exp. Sta. Bull. 554S.
- Turner, M. G., Wu, Y., Romme, W. H. & Wallace, L. L. (1993). A landscape simulation model of winter foraging by large ungulates. *Ecol. Modelling* 69: 163–184.
- Turner, M. G., Wu, Y., Wallace, L. L., Romme, W. H. & Brenkert, A. (1994). Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecol. Appl.* 4: 472–496.

- Vales, D. J. & Peek, J. M. (1990). Estimates of the potential interactions between hunter harvest and wolf predation in the Sand Creek, Idaho, and Gallatin, Montana, elk populations. In *Wolves for Yellowstone? Vol. II. Research & analysis*: 3.92–3.167. Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Van Soest, P. J. (1987). *Nutritional ecology of the ruminant*. Ithaca, N. Y.: Cornell Univ. Press.
- von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biol.* 10: 181–213.
- von Mises, R. (1957). *Probability, statistics and truth*. New York, N. Y.: Macmillan Co.
- Weaver, J., Escano, R., Mattson, D. & Puchlerz, T. (1986). Cumulative effects process for the Yellowstone ecosystem. In *Proceedings – grizzly bear habitat symposium*: 234–246. Contreras, G. & Evans, K. (Compilers). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-207.
- Weaver, T. & Forcella, F. (1986). Cone production in *Pinus albicaulis* forests. In *Proceedings – conifer tree seed in the inland mountain west symposium*: 68–76. Shearer, R. C. (Compiler). Ogden, Ut.: U. S. For. Serv. Gen. Tech. Rep. INT-203.
- Weisberg, S. (1985). *Applied linear regression*. (2nd edn). New York, N. Y.: John Wiley & Sons.
- Welch, C. A., Keay, J., Kendall, K. C. & Robbins, C. T. (1997). Constraints on frugivory by bears. *Ecology* 78: 1105–1119.
- White, D., Jr., Berardinelli, J. G. & Aune, K. E. (1998). Reproductive characteristics of the male grizzly bear in the continental United States. *Ursus*. 10: 497–501.
- Whittemore, C. T., Tullis, J. B. & Emmans, G. C. (1988). Protein growth in pigs. *Anim. Prod.* 46:437–445.
- Wielgus, R. B. & Bunnell, F. L. (1994). Sexual segregation and female grizzly bear avoidance of males. *J. Wildl. Manage.* 58: 405–413.
- Wold, H. (1956). Causal inference from observational data: a review of ends and means. *J. R. Stat. Soc. A* 119: 28–50.
- Worton, B. J. (1987). A review of models of home range for animal movement. *Ecol. Modelling* 38: 277–298.
- Worton, B. J. (1995). Using Monte-Carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manage.* 59: 794–800.

- Yates, F. (1953). *Sampling methods for censuses and surveys*. (2nd edn). New York, N. Y.: Hafner Publ. Co.
- Yellowstone National Park. (1997). *Yellowstone's northern range: complexity and change in a wildland ecosystem*. Mammoth, Wyo.: U. S. Natl. Park Serv., Yellowstone Natl. Park.
- Yoccoz, N. G. (1991). Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bull. Ecol. Soc. Amer.* 72: 106–111.
- Youmans, C. C. (1979). *Characteristics of pocket gopher populations in relation to selected environmental factors in Pelican Valley, Yellowstone National Park*. Bozeman, Mont.: M. S. Thesis, Mont. State Univ.