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Responses by grizzly bear population dynamics to certain environmental and biosocial factors

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To the Graduate Council:

I am submitting herewith a dissertation written by Stephen Frederick Stringham entitled "Responses by grizzly bear population dynamics to certain environmental and biosocial factors." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Michael R. Pelton, Major Professor

We have read this dissertation and recommend its acceptance:

Gordon Burghardt, Neil Greenberg, Anton Bubenik

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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and recommend its acceptance:

Gordon M. Burghardt

John W. Philpot

Accepted for the Council:

CW Minkel
The Graduate School

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RESPONSES BY GRIZZLY BEAR POPULATION DYNAMICS TO CERTAIN ENVIRONMENTAL AND BIOSOCIAL FACTORS

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Stephen Frederick Stringham
March 1985

DEDICATED TO

My father Robert Stringham
who set the standards of professional excellence, personal integrity,
and devotion which I have strived to match

My mother Joyce Stringham
My ladies Ann Stringham and Brenda Goldman
My Sisters and their families
Christine, Vladimir, Elizabeth, and Michael Nicholayeff
Jeanette Stringham
Helen, Pete, and Steve Strauss
Laura and Brian Lippencott
whose love has sustained me

My colleagues who set standards that made me stretch
Valerius Geist, Anton Bubenik, John Craighead,
Fritz Walther, Lynn Rogers and Dale McCullough

My professors and friends who nurtured my growth, especially
Clarence Howe, Neil Greenberg, John Philpot
Tom Cooper, Raul Valez, Alan Solbert

Through this dissertation,
the best within me salutes the best within you.

ACKNOWLEDGEMENTS

This dissertation is based on analysis, interpretation, and modeling of data collected by other investigators. So whatever my work with it has added to our understanding of bears, the bulk of the credit for these findings belongs to the people who have dedicated the mammoth effort required to collect and initially interpret the data. Those whose data has made the greatest contributions to the findings presented here are, alphabetically, Dr. John Beecham, Glen Cole, John Collins, Dr.s John and Frank Craighead, John Eiler, Lee Glenn, Dr. Charles Jonkel, Dr. Richard Knight, S. J. Miller, Clifford Martinka, Dr. Arthur Pearson, Dr. Michael Pelton, Dr. Harold Picton, Dr. Lynn Rogers, Harold Reynolds, and Dr. Robert Ruff. Also important was the sharing of new ideas about bears by those and other colleagues including Thomas Beck and Dr. Dale McCullough.

Success of this research depended upon generous assistance from numerous people. Chief among these are the members of my doctoral committee, Dr. Michael Pelton, Dr. Gordon Burghardt, Dr. Neil Greenberg, and Dr. John Philpot. Invaluable advice and encouragement was also given by Dr. Anton Bubenik, Dr. Dewey Bunting, Dr. Edward Clebsch, Stewart Coleman, Dr. Donald DeAngelis, Dr. Boyd Dearden, Dr. Stephen Ellner, Dr. Valerius Geist, Dr. Louis Gross, Dr. Jack Ingliss, Dr. Gerald McCracken, Dr. Robert Ramger, Dr. Gypsy Ranney, Dr. William Sanders, Dr. David Schmidley, Dr. Raul Valdez, Dr. Gerald Vaughan, and Dr. Fritz Walther. Crucial computer assistance was provided by

Bruce Delaney, Philip Gerachi, Robert Munchen, Virginia Patterson, and other personnel of the University of Tennessee Computer Services.

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Much of the data analyzed here deals with Yellowstone grizzlies; so it is appropriate to make special mention of the role of National Park Service personnel. Closure of the Yellowstone open-pit garbage dumps led indirectly to the deaths of numerous grizzlies and to lowered reproductive rate, increasing risk of extirpation of that population. For this, the National Park Service came under severe criticism, some justified, much not. Certain results presented here clearly demonstrate the adverse effects of dump closure on that population. However, that should not be construed as being even implicitly critical of the National Park Service. Whatever the failings of past management practices, NPS has succeeded in preserving the population and is continuing to make a devoted effort to that end. Whatever the pressures on the NPS administration to allow extirpation of the Yellowstone grizzly population, efforts by personnel directly responsible for preserving the bears reveal great dedication and effort, deserving of high commendation.

ABSTRACT

Based on analysis of previously published data, comparison among grizzly populations and among years within the Yellowstone poulation reveal that essentially all parameters of reproduction and recruitment (survivorship - net emigration) were positively correlated with food supply and nutrient-energy balance, but negatively correlated with densities of adult males and females. Although densities of cub litters and of cubs would be positively correlated with density of adults when adults are scarce, all available data is for cases where densities of adults were so high that the correlations were negative--indicating strong density dependence.

The forms of density dependence exhibited by Yellowstone grizzlies are exceedingly complex. When density of adult males was high, few cubs were produced, mainly daughters; these cohorts had low rates of recruitment to adulthood. By contrast, when adult males were scarce, many cub litters and cubs were born, mostly sons; these cohorts had high rates of recruitment to adulthood. There were also negative correlations between recruitment of recently weaned subadults vs. concurrent density of adult males.

Those findings are interpreted in terms of competitive reproductive strategies of adult males vs. females. (1) Aggression by adult males against immatures might benefit the males through (a) nutritive value of immatures which are eaten, (b) reducing current and future competition from victims for resources or genetic representation, or (c) increasing opportunities to mate with mothers of the immatures. (2) Females might minimize wastage of investment in offspring likely to be killed or prematurely exiled by the adult males. This could explain the negative correlations between (a) number, sex ratio, and recruitment rate (manifesting investment) per offspring vs. (b) adult male abundance and adult sex ratio. (3) The Fisher (1930) and Trivers-Willard (1973) hypotheses, respectively, also predict reciprocal adult-offspring sex ratios and corresponding levels of investment per cohort.

Presentation of findings on grizzlies is accompanied by review and analysis of comparative information on black and polar bears. An attempt is made to integrate the bulk of current knowledge on factors governing dynamics of bear populations in order to more clearly reveal its implications for theory and management, and to facilitate development of theoretical stock-recruitment and population models--models in which dynamics are controlled by food supply, densities of adult males and females, adult sex ratio, and age. Although these statistical results should be most applicable to grizzly populations where bears frequently aggregate in large numbers at food concentrations, basic features of the descriptive and theoretical models should be applicable to bear populations in general and perhaps to other taxa.

PREFACE

Bears have been the subject of much interest and study for generations. Important information was gathered by explorers, hunters, and naturalists as exemplified by Wm. H. Wright, Enos A. Mills, and Ernst T. Seton during the late 1800's and early 1900's. Among the earliest formal research was that conducted in Mt. McKinley (Denali) National Park, beginning in the 1920's, by Adolph Murie. But another 40 years passed before development of sophisticated, cost-effective apparatus and drugs for capturing, individually marking, tracking, censusing, and aging bears enabled ecologists to begin characterizing populations in enough detail to support quantitative analysis of population dynamics and behavior, and of the factors controlling them. In the ensuing 2 decades, the amount of available data has become enormous. Bear research has been further enhanced by increased exchange of bear information, largely through (a) symposia and publications sponsored by the International Association for Bear Research and Management (originally the Bear Biology Association. organized in 1977), and (b) the Bear Bibliography Project of Fred Dean and Diane Tracy.

The time has now come for broad synthesis of the bear information. This dissertation reviews most data on demography, focusing on those grizzly populations for which data collection was comprehensive enough for the parameters of reproduction and recruitment (survival minus net emigration) to be quantitatively related to one another or to the environmental and biosocial factors which control them. Comparative information on other bears is reviewed too. That extends work begun in the mid-1970's by Dr.s Lynn Rogers, Steve Herrero, Fred Bunnell, David Tait, Dale McCullough, and myself.

The text was written for readers familiar with basic terms and concepts in the branches of ecology dealing with demography, behavior, and physiology. The only terms defined are those otherwise subject to ambiguity. Numerical reasoning and results form the skeleton of the dissertation. But those results were graphed and the text written to be easily grasped even by readers whose understanding of mathematics is limited to elementary algebra and statistics. Chapter summaries are even more toned-down and streamlined.

This work was done to provide a more comprehensive view of what we already know about ecology, behavior, and dynamics of certain bear populations as well as implications of that for understanding different populations or species of bears or other taxa. It is intended to (a) alert researchers to the strengths and weaknesses of available information, (b) to more specific ways of addressing familiar questions, and to (c) new questions in need of answers. For example, the question "Does food supply control dynamics of bear populations" has been replaced with "How much do age- and sex-specific rates of reproduction and recruitment vary per unit of change in food supply? Under what circumstances do variations in population density or infrastructure have more impact on food supply per bear than do variations in supply per se?" This dissertation should also help to reveal how much untapped information remains in available data--only a fraction of which is represented here. Advancement of our field over the next decade could depend as much upon a more thorough treatment of existing data as on gathering new data. Our efficiency in testing hypotheses, answering basic questions, and solving pragmatic problems will depend directly upon how effectively we communicate amongst ourselves--researchers, managers, administrators, etc. Since the ultimate purpose of this dissertation is to facilitate our quest to better understand and manage bears, it should be thought of not as an endpoint but as an heuristic steppingstone.

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PART I: INTRODUCTION AND METHODS

CHAPTER 1

INTRODUCTION

1:I. OBJECTIVES

A key objective in the study of population ecology for any species is to determine how rates of reproduction and recruitment respond to variations in environmental factors (e.g., food supply) and biosocial factors (population density, infrastructure, distribution, and behavior). That is approached here for grizzly bears by review and analysis of data on reproduction and recruitment relative to those factors--as depicted with a flow chart in Fig. 1:1. Later on, each variable on that model shall be elaborated and many of their interrelationships shall be quantified by regression analysis on empirical data. Finally, the initial steps shall be taken towards derivation of theoretical mathematical models for some of those interrelationships so that they can be integrated into a dynamic simulation model. Although some results may be more-or-less specific to bears, others may be applicable to diverse taxa.

For convenience in this dissertation, all *Ursus arctos* are termed "grizzlies", irregardless of where in North America they occur. All *Ursus americanus* are termed "black bears."

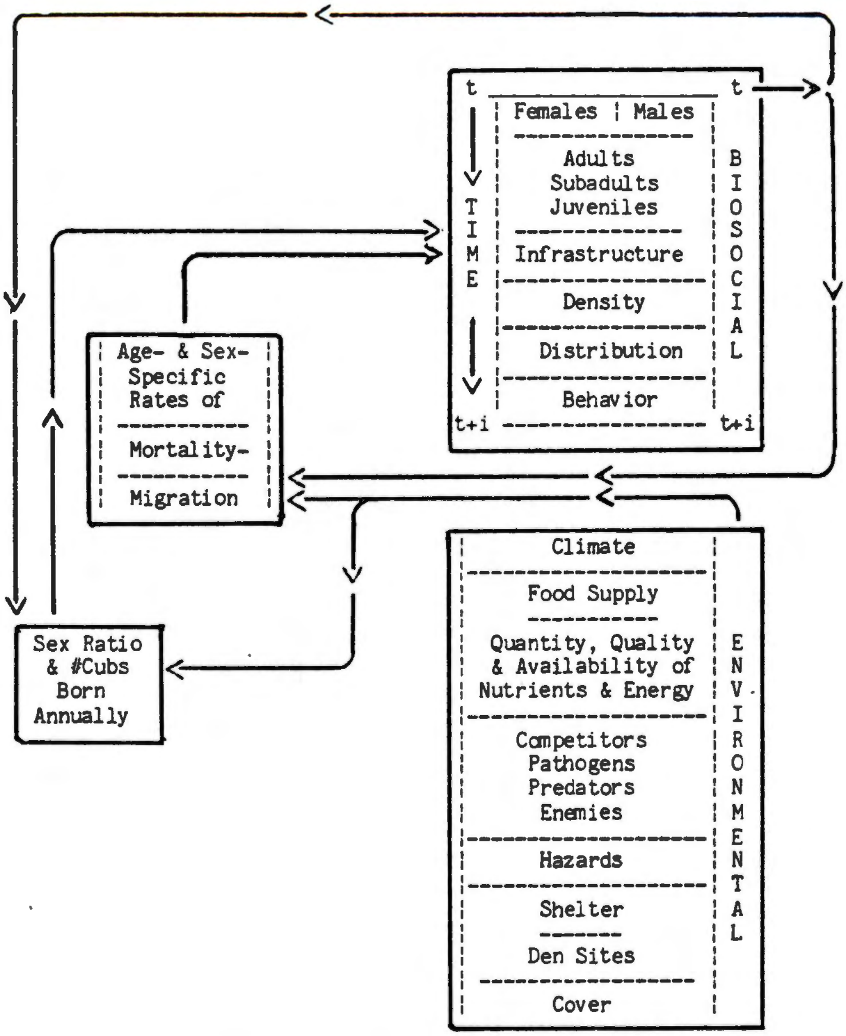


Fig. 1:1. Dynamics of a bear population as functions of biosocial and environmental factors. Dynamics refers here to changes over time (t to t+i) in characteristics of the population, including its infrastructure (age- and sex-class ratios), density, and spatio-temporal distribution of members. Biosocial factors include those characteristics of the population, as well as behavior of its members. (For more detail, see Fig.s 3:4, 4:2, 11:1, and 13:1).

1:I.A. Environmental Influences

It is well known that dynamics of mammal populations can be infuenced by a variety of environmental factors. Among these factors are, shelter, climate, food supply, competitors, predators, and pathogens. Only climate and food supply--largely through their combined influences on individual nutrient-energy balance (Fig. 1:2)--are known to have strong impacts on rates of natality or attrition (mortality + net emigration) for bears in North America (e.g., Rogers 1976, 1977, 1983, in prep.). Also, climate and food supply are the only environmental influences for which data are abundant enough to support detailed quantitative analysis. So attention here is focused on analyzing and modeling their roles.

1:I.B. Biosocial Influences

That productivity by a large mammal population can be limited by low density of adult females is obvious. So too is the fact that productivity can be limited if there are not enough adult males to impregnate all estrus females, or perhaps even if there are not enough to impregnate all of them during the optimal breeding season. The importance of such "density independent" density related effects is clear.

What is not clear is whether "density dependent" effects are comparably important. For example, does population density commonly become so high that it reduces food supply per adult female enough to limit the number of offspring she produces or her mean investment in

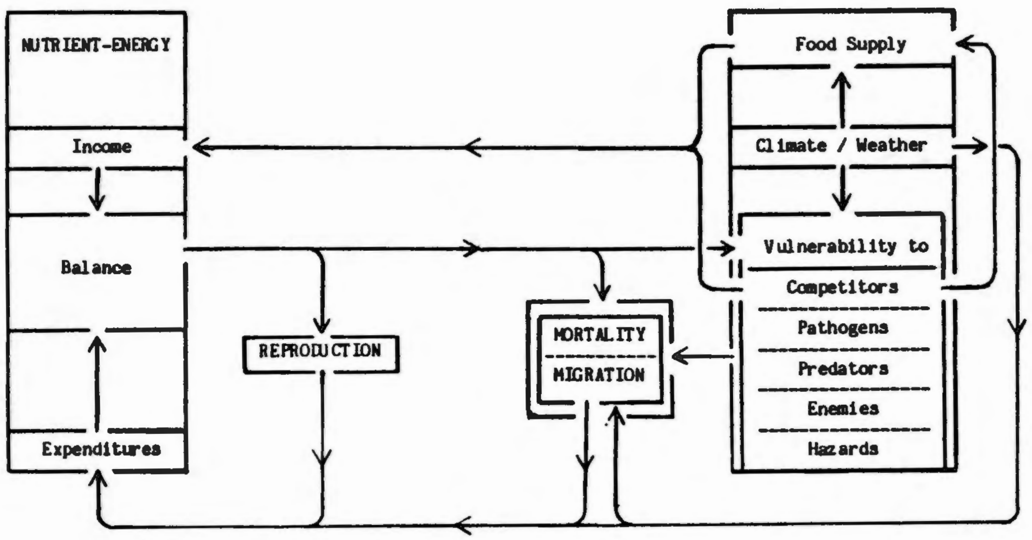


Fig. 1:2. Effects of various environmental factors on rates of reproduction, mortality, and migration, according to how those factors (a) are mediated by or (b) affect food supply and nutrient-energy balance of the bears.

each of them? Even though the occurrence and importance of density dependence in large mammals is still controversial, it seems to have been demonstrated in a number of cases. Among those are the studies on ungulates by McCullough (1979) and Houston (1982), that on cetacea by Allen (1981), and those on pinnipeds by Chapman (1961), Lett et al. (1981), Eberhardt (1981), and DeMaster (1981). Fowler et al. (1980) and Fowler (1981) review much of that literature; see also Tanner (1966).

Although densities of the entire population and of adult females within it are key variables in most density related population models (see Chapter 13), little consideration has been given to the specific effects of adult male density and behavior. Management practices, theories, and models generally assume that (a) males serve only to sire offspring, and that (b) so long as adult males are abundant enough to breed with all fertile females (e.g., see Allen 1981: Fig. 3), adult male density affects population dynamics and ecology in about the same ways as density of sterile females.

Nevertheless, numerous behaviors (roles) of males (e.g., protection of a male's own young and providing them with food, or eliminating offspring of rival males) could have strong influences on population dynamics and ecology (van Lawick-Goodall & van Lawick-Goodall 1970; Bubenik 1971; Hrdy 1974, 1979; Bertram 1975; Kleiman 1977; Parker 1978; Kleiman & Malcolm 1981; and Gubernick 1981; Hapgood 1979 has reviewed much of the literature). Furthermore, sport hunting has, to some degree, reduced relative density of adult males below pristine levels in many, perhaps most big game populations worldwide. In some grizzly populations, for instance, adult sex ratio is less than 1M:4F (Stringham 1980). In many ungulate populations, the ratio is far lower (see Stringham & Bubenik 1975; pers. comm. with numerous sources; see Verme & Ozoga 1981). The effects of these low sex ratios and the demographic roles of adult males under natural and human-altered conditions need to be determined for meeting the goals of both management and theory. Work by Snyder (1962, 1972) on woodchucks (Marmota m. marmota), Vandenbergh (1967, 1969, 1973), and Izard & Vandenbergh (1982) also provide important clues about compensatory sex ratios, maturation rates, and other phenomena which should be of keen interest to those concerned with how abundance and behavior of adult males affect dynamics of mammal populations.

Studies on some of these phenomena have already been initiated with certain ungulates. Experimental manipulations on age-sex class infrastructures in European populations of chamois (Rupicapra r.), roe deer (Capreolus c.), and red deer (Cervus elaphus), have enabled researchers to characterize qualitatively and quantitatively how behavior and relative density of adult males affect population dynamics for those species (Bubenik & Schwab 1975; Stringham & Bubenik 1975). Raul Valdez has compared dynamics and behavior of populations of wild sheep (Ovis spp.) in Iran which had been subjected to radically different levels of hunting pressure (Valdez & Stringham, in prep.). That coincides with studies by Valerius Geist (e.g., 1971) and Wayne Heimer (pers. comm.) on wild sheep in North America.

1:II. PREVIOUS STUDIES ON BEARS

1:II.A. Food Supply, Climate, and Nutrient-Energy Balance

There is abundant evidence that, in bears as in other mammals, rates of reproduction and offspring survival tend to be positively correlated with body weight, climate, or other indices for food supply or individual nutrient-energy balance (Rausch 1961; Hatler 1967; Jonkel & Cowan 1971; Collins 1974; Stirling et al. 1976; Rogers 1976, 1977, 1983, in prep.; Picton 1978; Russell et al. 1979; Beecham 1980a,b; Bunnell & Tait 1981; Knight et al. 1981; 1982; Eiler 1981, Hugie in press; Alt, pers. comm.). Most of that evidence was originally presented as simple comparisons for rates or levels of reproduction or survival between periods of good vs. poor conditions. Most sample sizes were too small to support statistical tests of significance for those differences in conditions (see Chapter 4). The regressions of cub litter size vs. climatic severity by Picton (1978) and of litter size vs. latitude by Bunnell & Tait (1981) are among the only published determinations of how any demographic parameter for bears varies per unit change in any index of nutrient-energy balance or food supply, or any other environmental influence. Details are reviewed and evaluated in Chapters 5 and 6.

1:II.B. Population Density, Infrastructure, and Behavior

Prior to 1962, nearly all data on bears concerning demographic roles of adult density and behavior came from opportunistic observations accumulated over more than a century. These suggested that adult males not only (a) compete for food and other resources against adult females and immatures, but (b) the adult males also sometimes kill immatures or exile them from their natal area, as well as (c) inhibiting immigration by other males (Chapter 11). This was considered detrimental to the populations, at least from the standpoint of management for hunter harvests locally.

Since 1962, several formal studies of social organization have yielded further insights on roles of adult males (Hornocker 1962; Jonkel & Cowan 1971; Stonorov & Stokes 1972; Frame 1974; Pearson 1975; Bledsoe 1975; Egbert & Luque 1975; Rogers 1976, 1977, 1983, in prep.; Egbert & Stokes 1976; Amstrup & Beecham 1976; Lindzey & Meslow 1977b; Lindzey et al., in press; Reynolds & Beecham 1980; Beeman & Pelton 1980; Garshelis & Pelton 1981). An especially thorough study on the demographic roles of adult males, involving experimental reduction of adult male density, was conducted on black bears by the Ruff-Kemp-Young team (Kemp 1972, 1976; Young & Kemp 1982; Ruff, in prep.).

Possible roles of adult male aggression in population regulation, and/or expected benefits to hunters from increased population productivity following reduction in adult male density, have been discussed by a number of biologists. They include Troyer & Hensel (1962), Craighead & Craighead (1967), Stokes (1970), Jonkel & Cowan (1971), Kemp (1972, 1976), Glenn (1975), Glenn et al. (1976), Egbert & Luque (1975), Egbert & Stokes (1976), Rogers (1976, 1977, 1983, in prep.), Reynolds (1976, 1980, 1981, in press), Stringham

(1980, 1983), Bunnell & Tait (1981), McCullough (1981), Young & Ruff (1982), Lindzey et al. (in press), LeCount (1982), and Taylor et al. (in press). It was the focus of a panel discussion by T. Larsen et al. (in Herrero 1972a:253-254). It was also considered in the 1974 National Park Service Draft Environmental Impact Statement for Yellowstone National Park grizzlies (NPS-RDEIS-YNP 1974). Furthermore, Stokes (1970) and Rogers (1976, 1977) have discussed the possibility that aggression from adult males might elevate physiological distress in subordinates, and thus reduce reproductive rate for females (which are usually subordinate to the adult males) and survival rate for their offspring.

The studies since 1962 indicate that the amount of spatio-temporal home range overlap varies greatly among populations and probably among habitat types within populations. It may also vary seasonally and annually as a function of abundance and distribution of foods and of conspecifics. In general, spatio-temporal home range overlap seems greater for males than for females. Since males are more likely than females to disperse far from the dam's home range, usually as subadults, males may learn the spatio-temporal locations of more transient, localized food sources, and thus forage over a wider range even as adults. The polygamous reproductive strategy of males would also favor having a large home range encompassing ranges of numerous adult females--only a fraction of whom breed each year. (Amstrup & Beecham 1976; Rogers 1977; Garshelis & Pelton 1981).

Adult males appear to be less tolerant of proximity by conspecifics than are adult females, in that they seem more likely to kill subadults, to exile resident subadult males, and to prevent immigration by alien subadult males. Greater dispersal by male than female subadults may be a consequence of differential behavior towards them by (a) adult males, including those courting their dam, (b) their dam herself, or (c) other adult females. For instance, subadult males may be more a target of aggression by adult males and possibly adult females. Whether that applies to murder of immatures as well as to exile, is not yet known, but is a possibility (see Chapter 11). Nevertheless, male subadults may exhibit greater "preference" than females for dispersal even when such social pressures are low (see Jonkel & Cowan 1971; Rogers 1977; Kemp 1976; Young & Ruff 1982). Intolerance by adult females for proximity of conspecifics, particularly males or non-kin females, might also tend to limit local population density, at least density of certain age-sex classes.

It is much less certain whether social intolerance by bears of any age-sex class limits density below levels imposed by food supply per bear or per unit bear-mass (Rogers 1976, 1977, 1983). There is some evidence that social intolerance and dispersal to marginal "habitat" by subadult males increases during periods when natural foods are scarce (Hatler 1967; Jonkel & Cowan 1971; Beeman & Pelton 1980; Garshelis & Pelton 1981). Food supply also limits reproduction and survival directly, as summarized earlier.

For these and other reasons, we do not yet know how strongly and in what ways population dynamics are affected by social intolerance. Even though resident adult male grizzly and black bears exile resident immatures, mainly males, we do not know how much that affects survivorship by the immatures or subsequent reproductive rates for populations that lose more migrants than they gain, or vice versa. Exiled immatures may be able to establish residency elsewhere. Likewise, even though adult males sometimes kill immatures, neither the frequency of that nor its the impact on population dynamics has been quantified.

According to Rogers (1983), among black bears, murder of immatures by adult males is probably rare, except perhaps when food supply is so poor that immatures are especially vulnerable due to debilitation, and adult males are more predatory on them due to hunger. (Vulnerability is also increased for bears in traps or which have recently been tranquilized; see Rogers 1983). Accordingly, Rogers considers variations in food supply to have had much more influence than variations in adult male abundance on rates of attrition by immatures in northeast Minnesota. Likewise, Beecham (1980a,b) attributes differences in levels of reproduction between 2 Idaho black bear populations--one hunted lightly, the other heavily--to differences in habitat quality, rather than to differences in densities or behaviors of the adult and subadult males, or to differences in other biosocial factors.

In black and grizzly bears, forced dispersal of subadult males may help regulate population density, particularly when density of resident adults is high. However, that would not seem effective for the more nomadic polar bears (Taylor et al., in press). By contrast, 2 other results of aggression by adult males--(a) murder of immatures, including subadults, and (b) dams with cubs avoiding prime habitat (where adult males are most common)--would seem likely to inhibit population growth when density becomes high in any of these 3 bear species (see Taylor et al. in press).

In addition to those direct observations on demographic roles of adult males and females, attempts have been made to use statistical analysis of demographic data to elucidate and quantify how per capita and annual rates of reproduction and recruitment in grizzly populations vary relative to densities of adult females and males. Stringham (1980) did this in terms of differences among populations. By contrast, Schaffer (1978, 1983), McCullough (1981), and Stringham (1983), did it in terms of variations over time within the Yellowstone population.

1:II.C. Population Models and Stock-Recruitment Models

In 1974, J. Craighead et al. published predictions for trends in density of the Yellowstone grizzlies, based on a deterministic model which assumed that population growth rate was density independent. Knight & Eberhardt (in press) have recently produced a density independent stochastic model and set of projections for

Yellowstone grizzlies; it treats variations in litter size and other demographic parameters as random events. In both of those models, the focus of attention was on (a) direct effects by demography (density and infrastructure) on dynamics, rather than on (b) the environmental or biosocial factors controlling dynamics via demography. Density independent population models devised for other populations or for bears in general, have been published by Stirling et al. (1976), Miller et al. (1981), and Sidorowicz & Gilbert (1981).

By contrast, density dependence has been incorporated into the stochastic model of the Yellowstone population done by Schaffer (1978, 1983), and into the deterministic models of that population done by Bunnell & Tait (1981) and McCullough (1981). The models by Schaffer and by Bunnell & Tait are computer simulation models which incorporate at least 1 density dependent (negative feedback) equation based on total adults or of adult males. McCullough's (1981) original models (e.g., of stock-recruitment relations) were derived statistically, but have since been extended for simulation of population dynamics (in press).

Models presented by Stringham (1980, 1983) were also statistically derived and deterministic. The 1983 models differ from McCullough's in (a) some of the age-sex classes chosen for analysis and modeling, (b) some of the parameters of reproduction and recruitment tested, (c) the kinds of mathematical forms used, and in (d) some of the implications derived from them.

1:II.D. Summary

Field studies on bears have provided evidence that rates of reproduction and recruitment are positively correlated with indices for food supply and nutrient-energy balance, and that they are negatively correlated with abundance of adult males. Some progress has also been made towards quantifying the amount of change in those rates per unit change in food supply, nutrient-energy balance, abundance of adult males, or other environmental and biosocial influences. Linear models of responses by litter size to (indices) of nutrient-energy balance have been published by Picton (1978) and Bunnell & Tait (1981). Models of responses to abundances of adults (males, females, total) have been published by Schaffer (1978, 1983), Stringham (1980, 1983), and McCullough (1981).

1:III. THIS STUDY

The value of those pioneer efforts not withstanding, more complex models are needed on both environmental and biosocial factors, individually and in combination. Furthermore, existing reviews on these subjects, even the recent comprehensive paper by Rogers (1983) incorporate little of the information on grizzly bears. Indeed, most of the grizzly literature still awaits analysis in terms of responses by population dynamics to environmental and biosocial factors.

To meet those needs, at least in part, has been the goal of the research presented here. The attempt was made to review virtually all available data on demography of bear populations and to derive as much information as possible from that data, to determine what it can reveal about responses to environmental and biosocial factors for bears and other species. Those results should also (a) ease development of corresponding simulation models, and (b) facilitate continuing field research and management.

Because the results presented are highly complex, and to avoid undue redundancy, the text is extensively cross-referenced. When the reference is to information in another chapter, both the chapter and section are designated (e.g., Chapter 9:II.C.2.c). However, within a given chapter, only the section number is designated (e.g., Section II.C.2.c). All major sections are listed in the Table of Contents.

To further reduce possible difficulties stemming from complexity and detail of statistical arguements, Chapters 4-13 are each followed by a narrative summary. Once the summary has been read, the reader should be able to follow the text of each chapter readily even without grasping all of the statistics. Accordingly, it is recommended that the reader begin by skimming all of the summaries in sequence, then reading each summary before as well as after reading each chapter.

To reduce length of this dissertation, about half of the findings have been deleted. But it is intended that they will eventually be published, and are cited as "Stringham, in prep."

CHAPTER 2

STATISTICAL METHODS

Since the material presented here includes only review and analysis of data available in the literature, the only "methods" used were statistical. Those were (1) Pearson Product-Moment and Spearman Rank correlation, (2) Least-Squares/Minimum-Variance regression, (3) Analysis of Variance, (4) Analysis of Covariance, (5) Principle Component Analysis, and (6) Student's t-test. All were done using SAS-79 (Statistical Analysis System; Helwig & Council 1979) programs on the IBM 370 computer of the University of Tennessee, Knoxville.

Numerous references are made here to "autocorrelation" and "autoregression." Conventionally, the term "autocorrelation" refers to the relationship between the value of factor X at time t vs. its value at some other time t+i. For example, one might test for an autocorrelation between population density during each year vs. that for the previous year or several years, to determine whether data on recent densities provides useful predictions about future densities. Likewise, to derive a predictive equation, one might autoregress the value at time t vs. its value at t+i.

For want of better alternative terms, "autocorrelation" and "autoregression" are used here for referring instead to the relationship wherein one function of a variable is correlated with or regressed against another function of that same variable, even without any time lag. For example, one might regress density of cubs per adult female vs. density of adult females in the population (*#C/AdF vs. #AdF*). Or, one might regress population density vs. food supply per unit area (*N/A vs. FS/A*). These regressions are of forms *Y/X vs. X* and *Y/Z vs. X/Z*, respectively. Particular attention is paid to autocorrelative relationships because of the artifacts which they tend to manifest, such as exaggeration of the correlation coefficient. This is discussed in Chapters 6:X and 9:I.C.

CHAPTER 3

DEMOGRAPHIC PARAMETERS & INDICES

"Demography" refers to the study of populations, particularly in terms of overall density and infrastructure--the age-sex class distribution, the proportion of members in each age-sex class. Changes in density and infrastructure constitute population dynamics, which result from variations in rates of reproduction and recruitment, caused by environmental and biosocial influences. In preparation for analyzing those influences, this chapter considers each of the major parameters of reproduction--whelping rate, cub litter size and sex ratio, etc.--and recruitment, first individually, and then in terms of their qualitative interrelationships. That is followed by derivation of compound indices for productivity, fecundity, and reproductive vigor.

3:I. SIMPLE PARAMETERS

3:I.A. Timing of Censuses

In the populations from which data comes for this analysis (Fig. 3:1), nearly all bears were censused during summers, usually June-August. Because most young are born in January or February, they average about 6 months (0.5 year) of age at mid-summer; hence, that is the average age assumed at the time of censusing.

Fig. 3:1. Approximate locations of grizzly bear populations for which data are available on reproduction or recruitment, and infrastructure or body weights.

1. Western Brooks Range
2. Eastern Brooks Range
3. Northern Yukon Territory
4. Northwest Territories
5. Chignik-Black Lakes
6. Kodiak Island
7. McNeil River Game Sancutary
8. Nelchina Basin
9. Southwestern Yukon Territory
10. Admiralty Island
11. Glacier National Park, Canada
12. Yellowstone National Park

3:I.B. Reproduction

The value for each reproductive parameter obtained from censuses each year is a product of rates of (a) ovulation, conception, implantation, and natality, as well as the rate of (b) subsequent mortality between birth and censusing. From a pragmatic standpoint, effects of mortality on values of reproductive parameters between conception and age 0.5 year are usually indistinguishable from correspondingly lower values at conception. So reproductive levels at censusing cannot be described as direct measures of natality. But they can be described by the less specific term "reproduction" since it is not necessarily synonymous with any of the terms "fertility," "fecundity," or "natality." Instead, "reproduction" usually refers to the number of offspring found per year at the earliest age that they can be censused, whether pre- or postnatally--irrespective of whatever mortality may have occured between conception and censusing.

Hence, for purposes of this analysis, variables interpreted as reproductive parameters--measured at an average age of about 6 months, conventionally denoted as "0.5 year"--include (1) cub density [#C], (2) whelping level and rate, (3) interbirth interval, (4) mean cub litter size [number of cubs per litter, C/L], and (5) cub sex ratio [percent male cubs, %MC]. Other reproductive parameters include ages at weaning [AW], puberty [AP], and first whelping [AFW]. (See Appendix A for a key to all abbreviations and symbols).

Recall that "density" means "number per unit area." For any single population, area is essentially constant; so "density" differs from "number" only in scale, and not even that where the area is defined as being of unit size, to simplify discussion or calculation. Only when density is compared among populations occupying areas of different size does number per unit area have to be distinguished from absolute number censused (see Chapter 7:I).

3:I.B.1. Whelping Level and Rate

"Whelping" refers to parturition or birth. Whelping level refers to the density of adult females whelping per year, and thus density of litters produced [#L]. By contrast, whelping rate refers to the proportion of all adult females in the population whelping during a given year [#L/AdF]. Where specified, whelping rate can also refer to the proportion of only fertile adult females whelping. "Fertile" females are defined as being those likely to whelp during the given year since they were mature and likely to have mated during the previous breeding season--judging, for instance, from the fact that they were not lactating then (see Chapter 5:II.B.2.).

3:I.B.2. Interbirth Interval and Age at Weaning

Interbirth interval [IBI] is the mean interval until females that whelped in year $\underline{t}$ whelped again. The interbirth interval for mothers which rear at least 1 cub of the litter to weaning can be split into (a) the birth-to-weaning interval [BWI], and (b) the weaning-to-next-birth interval [WNBI]; that is:

$$\mathrm{IBI} = \mathrm{BWI} + \mathrm{WNBI}$$

"Weaning" refers here not just to cessation of lactation, but also to dissociation of offspring from their mother (see Stringham 1974). The birth to weaning interval may be inversely related to cub maturation rate (e.g., Jonkel & Cowan 1971). If mean interbirth interval is n years long, then mean whelping rate is roughly 1/n (e.g., about 33% for a population whose mean interbirth interval is about 3 years). However, that inverse relationship is not exact, as demonstrated by the Yellowstone grizzly data: Mean #L/AdF = 32.8%, yet 1/IBI = 1/3.21 years = 31.2%. That inexactness, which is small in this case, is due to a number of factors, probably including (1) lack of interbirth interval data on 64% of the YNP litters censused, (2) attrition between years by some resident adult females, and (3) recruitment of new adult females by maturation or perhaps immigration.

3:I.B.3. Generation Length and Age at Puberty

The interval from birth of a female cub until birth of her own first offspring, that is, her age at first whelping, is also termed her generation length (G). Generation length can be subdivided into (a) the birth-to-puberty interval, which equals the age at puberty [AP], and (b) the puberty-to-first-whelping interval [PFWI]:

$$G = AP + PFWI.$$

Age at puberty is the mathematical inverse of maturation rate to puberty. So generation length also tends to be inversely related to maturation rate. A positive correlation between age at puberty vs. latitude (AP vs. Lat), represents a negative correlation between maturation rate vs. latitude ($1/AP$ vs. Lat), and vice versa (see Chapter 5:I.A).

3:I.C. Recruitment and Attrition

All young born during a given year, for instance 1960, are termed the 1960 year-class birth *cohort* or, more succinctly, the 1960 cohort. That cohort's average age when censused in 1961, 1962, and 1963 would respectively be 1.5, 2.5, and 3.5 years. Density of recruits in each cohort (cohort size) at any age (a) or time (t) is also termed "recruitment" to then (R_a). Loss from a cohort between specific ages or times is termed "attrition" ($A_{a \text{ to } a+1}$), whether loss is due to mortality or emigration. If immigration to a specific area by a particular cohort exceeds emigration, then local recruitment can exceed 100%. That is,

Recruitment = Survivorship + net Immigration

Attrition = Mortality + net Emigration

$$
\begin{aligned}
\#A_{a \text{ to } a+1} &= R_a - R_{a+1} \\
\#A_{0.5 \text{ to } 2.5} &= R_{0.5} - R_{2.5} \\
\%A_{0.5 \text{ to } 2.5} &= (R_{0.5} - R_{2.5}) / R_{0.5} \\
&= (\#A_{0.5 \text{ to } 2.5}) / R_{0.5}
\end{aligned}
$$

To avoid confusion, number/density lost during any year is termed attrition "level" (#A), whereas the proportion lost is termed attrition "rate" (%A). Here, the term "cohort" is never used to mean a broader age-sex class (e.g., the "adult cohort").

Analyses are done in terms of recruitment and attrition, rather than in terms of survivorship, mortality, and migration. For recruitment and attrition can be calculated directly from annual infrastructural data. But the extent to which recruitment and attrition are governed by mortality vs. migration is obscure. (See Tables 3:1 to 3:4 for data on reproduction and recruitment in bear populations).

3:I.D. Population Infrastructure

Mean infrastructures for several grizzly populations are reviewed in Table 3:5. Tables 3:6 and 3:7 review annual values for infrastructures of the Yellowstone grizzly population and for a Minnesota black bear population.

3:I.D.1. Age- and Maturity-Classes

"Cubs" are less than 1 year old. Yearlings are 1 to 2 years old. All non-adult bears, including cubs and yearlings, are "immatures." All immatures still accompanying their dam and dependent upon her directly are "juveniles." Among grizzlies, juveniles are almost always under 3.5 and usually under 2.5 years old; maximum ages for juvenile black bears are typically 1 year less. For most grizzly populations, 3- and 4-year-olds are termed "subadults" (preadolescents), and all older bears "adults."

There are, however, 2 exceptions to the latter rule (Table 3:5): (a) Grizzly bears in the Northwest Territories at ages 5 and 6

Table 3:1. Reproductive parameters (mean values) for wild populations and captive grizzly bears.*

Habitat Type and Population	Generation Length (G)	Interbirth Interval (IBI)	Litter Size (C/L)	Productivity** (C/L/IBI) (= Pr)	Fecundity* Pr*%FC	Reproductive** Vigor (RIV)
COASTAL						
McNeil River[1] Game Sanctuary	6	3.6	2.1	0.58	0.264	-2.28
Kodiak Island[2]	5	3	2.23	0.74	0.337	+0.70
Chignik-Black[3]	5	3	2.20	0.73	0.332	+0.60
INLAND						
Western[4] Brooks Range	7.9	4.1	1.98	0.48	0.220	-4.29
Eastern[5] Brooks Range	10.1	4.2	1.78	0.42	0.193	-0.700
Northwest[6] Territories	8**	≥3.8**	1.83	≤0.48	≤0.218	≤-4.89
Southwestern[7] Yukon Teritory	≥7.8**	4**	1.7**	0.42	0.193	≤-5.68

Table 3:1. (Continued)

Habitat Type and Population	Generation Length (G)	Interbirth Interval (IBI)	Litter Size (C/L)	Productivity** (C/L/IBI) (= Pr)	Fecundity* Pr*%FC	Reproductive** Vigor (RIV)
INLAND						
Northern[8] Yukon Territory	8**	4**	1.8**	0.45	0.205	-5.35
Glacier National[9] Park, Canada	≥5	≥2.8	2.0	≤0.71	≤0.323	≤+0.40
Yellowstone[10] National Park 1959-70	5.81**	≥3.2	2.18**	≤0.68	≤0.309	≤-0.63
CAPTIVES						
Europe[11]	3-4	2	2.05	1.02	0.464	+5.67

* After Stringham (1980:Table 2) and Bunnell & Tait (1981:Table 3).

** Calculated from data provided by the author.

Table 3:1. (Continued)

[1] Glenn (1973), Glenn et al. (1976). Glenn (1973) gave a figure of 2.1 for cub litter size; this was misprinted in the 1976 paper as 2.5.

[2] Hensel et al (1969); some of the data also came from the Alaska Peninsula.

[3] Glenn (1975, pers. comm.), preliminary results.

[4] Reynolds (1980, 1981, in press).

[5] Reynolds (1976, in press).

[6] Miller et al. (1981)

[7] Pearson (1975). Data permit calculation only of a minimum figure of 3 years for interbirth interval. But for cases where litters survived until weaned, intervals of 4 years are more likely, judging from supplementary data, including that on the northern Yukon Territory population.

[8] Pearson (1976).

[9] Mundy & Flook (1973). Apparently, most of the reproductive data comes from Glacier National Park, Canada; but some may have come from other Canadian "Mountain Parks."

[10] Craighead et al. (1969, 1974, 1976).

[11] Dittrich & Kronberger (1963).

Table 3:2. Parameters of reproduction and recruitment for Yellowstone grizzlies, annual values for 1959-81.*

Year	Inter-** birth Interval (IBI)	(n)	% Whelping Rate (#L/AdF)	Whelping Level (#L)	Cub Litter Size (C/L)	Cub Sex Ratio (%MC)	(n)	Cohort Size at				
								0.5 (#C)	1.5 (#Y)	2.5	3.5^1 & 4.5	5.5^2
1959	3.50	2	31	14	1.86	50	4	26	15	17	25	15
1960	2.50	2	36	17	2.06	67	6	35	17	9	19	-8
1961	3.25	4	30	13	2.31	46	13	30	13	11	23	7
1962	2.80	5	41	17	2.29	78	9	39	29	30	45	1
1963	3.40	5	37	16	2.50	86	7	40	30	34	26	25
1964	3.17	6	23	11	2.18	67	6	24	20	17	25	20
1965	3.75	8	44	19	2.11	100(75)^3	1	40	36	23	24	10
1966	3.43	7	35	15	2.13	50(62)	2	32	24	15	31	
1967	3.00	5	30	12	2.50	45	11	30	19	18		
1968	3.25	8	28	13	2.46	54	13	32	27	15		
1969	3.00	3	31	14	2.00	--(56)	0	28	18			
1970	2.43	7	27	12	1.75	50	6	21				
1971				16	1.94			31				
1972				11	2.00			22				
1973				15	1.80			27				
1974				15	1.73			26				
1975				4	1.50			6				
1976				17	2.06			35				
1977				13	1.92			25				
1978				10	1.90			19				
1979				13	2.00			26				
1980				9	2.11			19				
1981				13	1.69			22				

Table 3:2. (Continued)

* Data from J. Craighead et al. (1969, 1974) for 1959-70; Cole (1974) for 1971-73; and Knight et al. (1982) for 1974-81. Values from Knight et al. for 1974-81 are so-called "unduplicated samples"; that is, they exclude any observation thought to be a duplicate on any individual or family.

** Calculated from data provided by J. Craighead et al. (1969).

[1] Combined density of 3.5- and 4.5-year-olds from 2 consecutive cohorts.

[2] Calculated from data provided by J. Craighead et al. (1974) as descried in Appendix B. This is not biased by the fact that the value for the 1960 cohort is negative; Since this is only an index, relative values are what is critical, not the exact values themselves.

[3] Where the sample size for cub sex ratio was based on no more than 2 cubs, the observed ratio was considered meaningless and a surrogate ratio was estimated from the relationship of cub sex ratio to cub density (see text).

Table 3:3. Mortality for Yellowstone grizzlies, annual values.*

	Adults				Immatures				Age Unknown				
Year	M	F	?	Sum	M	F	?	Sum	M	F	?	Sum	Total
1959	5	1	1	7	2	2	0	4	0	0	1	1	12
1960	3	4	2	9	4	2	7	13	1	0	1	2	24
1961	1	1	1	3	7	4	4	15	1	1	1	3	21
1962	1	4	0	5	4	5	1	10	0	0	0	0	15
1963	2	3	0	5	4	2	2	8	2	0	0	2	15
1964	3	1	0	4	4	1	3	8	0	0	0	0	12
1965	2	3	0	5	6	2	0	8	1	0	1	2	15
1966	1	0	0	1	5	0	2	7	1	0	4	5	13
1967	2	3	2	7	6	1	3	10	9	11	6	26	43
1959-66	18	17	4	39	36	18	19	73	6	1	8	15	127
1959-67	20	20	6	46	42	19	22	83	15	12	14	41	170
1968	9	2	1	12	2	3	1	6	0	0	3	3	21
1969	8	6	0	14	3	3	1	7	1	1	0	2	23
1970	10	13	0	23	11	11	5	27	2	0	1	3	53
1968-70	27	21	1	49	16	17	7	40	3	1	4	8	97
1971	15	11	1	27	4	6	1	11	5	0	5	10	48
1972	10	7	1	18	3	3	2	8	0	0	1	1	27
1973	3	3	0	6	2	2	0	4	0	0	7	7	17
1971-73	28	21	2	51	9	11	3	23	5	0	13	18	92
1968-73	55	42	3	100	25	28	10	63	8	1	17	26	189

* After J. Craighead et al. 1974: Table 10.

Table 3:4. Parameters of reproduction and recruitment for Minnesota black bears, annual values for 1969-77.*

Year	% Whelping Rate (#L/AdF)	Whelping*[1] Level (#L)		Cub*[1] Litter Size (C/L)	Cub* Sex Ratio (%MC)	Cub Density (#C)	Cub Recruitment (%)
	N+R	N+R	R	R	R	R	R
1969							100
1970	44	7					83
1971	47	8	4.7	2.98	57.1	14	95
1972	46	11	5.5	2.54	64.3	14	62
1973	35	6	4.2	3.33	50.0	14	79
1974	68	15	8.2	1.84	40.0	15	71
1975	29	6	4.1	3.69	60.0	15	50
1976	27	6					81
1977	32	6					

* Data from Rogers 1977: Tables 3 and 8.

[1] Figures for cub litter size and number of cub litters are rough estimates calculated as follows:

#L = #AdF * #L/AdF
C/L = #C/#L

In the table, above, R = residents, N = non-residents. Rogers (Table 8) provided data from which the number of combined resident and non-resident females with litters could be calculated directly from the information on whelping rate and number of resident and nonresident adult females sampled. The number of just resident females whelping (#L) was estimated by multiplying total number of resident females by the proportion of resident plus nonresident adult females that whelped. Then these figures were divided into those for number of resident cubs to estimate litter size. Note that the figures for numbers of resident females and cubs are for June, that is about age 0.5 year for the cubs; the same is thus true for cub sex ratio.

[2] Percent of cubs in year t recruited as yearlings in t+1. It is not certain whether this refers to survivorship from about March to March or June to June, the but former seems to be implied.

Table 3:5. Infrastructure of North American grizzly bear populations.*

Habitat Type & Population	Latitude (°N)	Cubs	Yearlings	Older Immatures	Adults	Male Adults	Female Adults	Adult Sex Ratio (%MC)
<u>COASTAL</u>								
McNeil River[1] Game Sanctuary	59.0	15.0 (9.7)	9.3 (6.0)	13.5 (8.7)	62.1 (40.0)	27.4 (17.7)	34.7 (22.4)	44.2
Kodiak Island[2]	57.5	25.8 (42)	22.1 (36)	27.0 (44)	25.1 (41)	5.5 (9)	19.6 (32)	22.0
Chignik-Black[3] Lakes	56.0	25.0 (140)	15.0 (84)	30.2 (169)	29.7 (166)	4.1 (23)	25.6 (143)	13.9
<u>INLAND</u>								
Western[4] Brooks Range	69.0	17.6 (19)	12.0 (13)	25.0 (27)	49.1 (53)	21.3 (23)	27.8 (30)	43.4
Eastern[5] Brooks Range	69.0	-------32.3--------- (32)			67.6 (67)	33.3 (33)	34.3 (34)	49.3
Northwest[6] Territories	65.0	14.3 (5)	10.4 (4)	24.2 (9)	51.1 (19)	21.4 (8)	29.7 (11)	42.1
Southwestern[7] Yukon Territory	61.0	7.3 (3)	17.1 (7)	31.7 (13)	43.9 (18)	24.4** (10)	19.5** (8)	55.6
Yellowstone[10] National Park 1959-70	45.0	17.5 (31.4)	12.6 (22.6)	24.5 (43.8)	45.6 (82.0)	21.1 (37.7)	24.5 (43.8)	46.0

* Figures given are proportion and number ( ) of bears in each age-sex class. After Stringham 1980.

** Rough estimates from data provided by the author.

[1-10] See footnotes in Table 3:2 for references.

Table 3:6. Infrastructure of the Yellowstone grizzly population, annual values for 1959-70.*

	Number of Bears in Age-Class (Years)								
Year	Cub	1	2	3&4	5	≥5[1]	≥5M[2]	≥5F[2]	Total
1959	26	23	17	0	--	88	43	45	154
1960	35	15	5	12	21	102	55[3]	47	169
1961	30	17	17	23	-14	79	35	44	166
1962	39	13	9	35	-17	59	18	41	155
1963	40	29(30)[4]	11	25	18	72	29	43	177
1964	24	30(34)	30	19	15	82	34	48	185
1965	40	20	34	23	-8	70	27	43	187
1966	32	36	17	45	7	72	29	43	202
1967	30	24	23	26	1	72	31	40[3]	175
1968	32	19	15	25	15	90	44	46	181
1969	28	17	18	24	20	98	53	45	195
1970	21	18	15	31	10	94	49	55	179

* Data from J. Craighead et al. (1974).

[1] Number of 5-year-olds was estimated from the change in adult abundance and from number of known adult mortalities each year, as described in Appendix B. The actual numbers calculated are only approximations; but the pattern of variation from year to year in this index should be at least loosely correlated with variation in actual numbers of 5-year-olds.

[2] Numbers of adult males and females were given by J. Craighead et al. (1974) only for 1964-70. Those for 1959-63 were estimated from the equation derived by regressing adult male abundance vs. total adult abundance for 1964-70, as described in the text.

[3] The 1960 datum for adult male density seems anomalously high, as discussed in Chapter 9. The datum for adult female density during 1967 is anomalously low. For that year, J. Craighead et al. (1974: Table 1) reported 72 adults, yet only 31 adult males and 40 adult females, suggesting that sex of 1 adult could not be determined. If that adult of unknown sex was female, that might help explain why the reported density of adult females seems anomalously low during 1967, judging from correlations between adult female density vs. other parameters. Hence, the correlation between densities of adult males vs. females is 0.669 (P:2t=0.02) if the value for density of adult females in 1967 is 40, but 0.692 if it is 41. There are corresponding

Table 3:6. (Continued)

anomalies for relationships between whelping rate (#L/AdF) vs. controlling factors, including the index for food supply (Chapter 5) and population biomass (Chapter 9).

[4] In these cases, density of 2-year-olds in year t+1 exceeded density of yearlings in year t (1963, 1964). Although some immigration might have occurred, this could alternately be due to sampling error. Unless adjustments are made for this, analyses of recruitment and attrition are perturbated. So calculations presented here assume 30 yearlings in 1963 and 34 in 1964.

Table 3:7. Food supply and infrastructure for a Minnesota black bear population, 1968-76.*

Year	Food Supply	Number of Bears in Age-Sex (M:F) Class						
		Cub	1	2	3	4	5	≥5
1968	Low							
1969	High							
1970	High							
1971	High	8:6	3:6	3:3	0:2	2:4	2:0	4:10
1972	Low	9:5	6:6	5:6	3:3	0:2	3:4	6:12
1973	High	7:7	8:4	6:6	4:5	2:2	0:1	5:12
1974	Low	6:9	5:4	8:4	3:5	3:4	3:1	7:12
1975	Low	9:6	4:6	3:4	2:2	1:4	4:3	9:14
1976	Low							

* Data from Rogers (1977).

were included as subadults by Miller et al. (1981). They did not specify separately densities of 3- and 4-year-olds vs. $\geq$5-year-olds. (b) Mundy & Flook (1973) classifed all bears $\geq$4 years old as adults.

Most "adults" have completed puberty and are physiologically capable of reproducing (see Erickson 1964; Erickson et al. 1968; Hensel et al. 1969; J. Craighead et al. 1969; Pearson 1975). "Adults" which have not yet reached peak reproductive capability and body size are "adolescents"; those at peak capability and size are "primes"; those past prime are "senescents" (for details, see Stringham, in prep., and Egbert & Stokes 1976).

The infrastructural data provided by Rogers (1977) for Minnesota black bears (Table 3:7) includes the number of residents of each sex separately for each age each year. By contrast, the infrastructural data of J. Craighead et al. (1974) on Yellowstone grizzlies (Table 3:6) lumps data on 3- & 4-year-olds and on $\geq$5-year-olds (adults). That constrains analysis of recruitment rate from age 0.5 to adulthood for YNP grizzlies. To help overcome that constraint, recruit density within each cohort at age 5.5 years was estimated, as described in Appendix B.

3:I.D.2. Sex Ratios

Another limitation on the infrastructural data for Yellowstone grizzlies is the lack of separate data for males vs. females in most age-classes. Sex ratio data for an average of about 20% of the cubs was provided by J. Craighead et al. (1974) for most years; ratios for the sampled cubs are used here as rough indices for sex ratio among all cubs in each cohort (Table 3:2a). Since the proportion of cubs sexed is small, results are correspondingly tentative.

Cub sex ratio was estimated during 3 years when sample size was too small to be useful (1965 1 cub, 1966 2 cubs, 1969 0 cubs). That estimate was made through use of the equation obtained by regressing cub sex ratio vs. cub density for the other 9 years.

$$\%MC = 12.0 + 1.57 * \#C$$

Cub density statistically accounts for 48% ($P{:}2t = 0.04$) of the variance in cub sex ratio (Fig. 3:2). Multiplication of cub sex ratio by total cub density yields estimates for densities of male and female cubs each year:

$$\#MC = \#C * \%MC / 100$$

$$\#FC = \#C - \#MC$$

If one is to judge from these indices for sex ratio and densities of male and female cubs, most variation in total cub density was due to variation in male cub density ($r^2 = 51\%$, $P{:}2t=0.01$, Fig. 3:2), just as for adults (Fig. 3:3). The standard deviation for estimated density of male cubs is more than twice that for females (8.4 vs. 3.8) among the 9 years with usable data during 1959-70.

Annual sex ratio data was not provided by J. Craighead et al. (1974) for older immatures; but it was provided for adults during 1964-70 (Table 3:5). As was pointed out by McCullough (1981), the equations derived by regressing adult male density or adult sex ratio

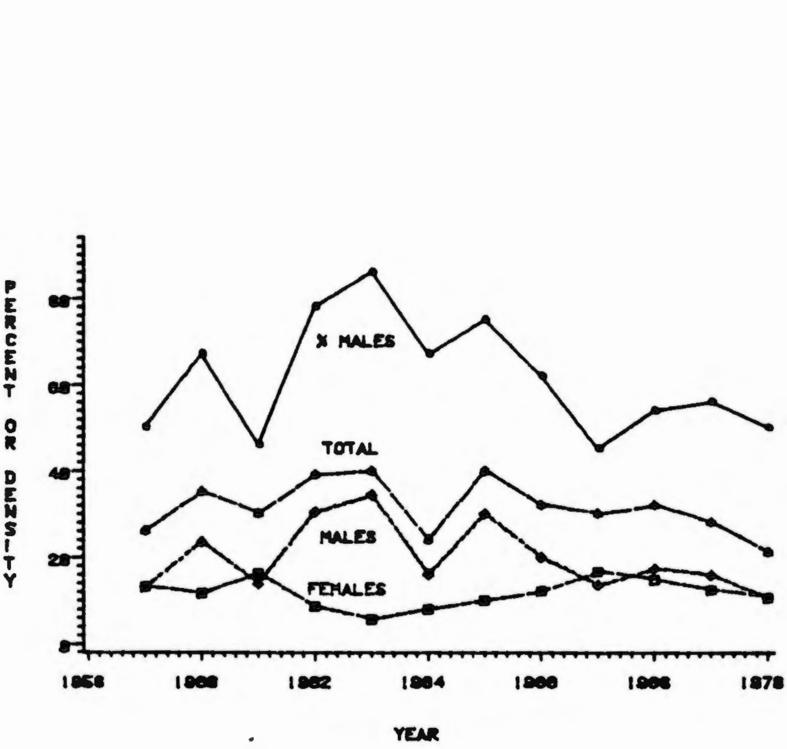


Fig. 3:2. Annual variations in cub sex ratio and in densities of cubs--total, males, and females--among Yellowstone grizzlies (1959-70).

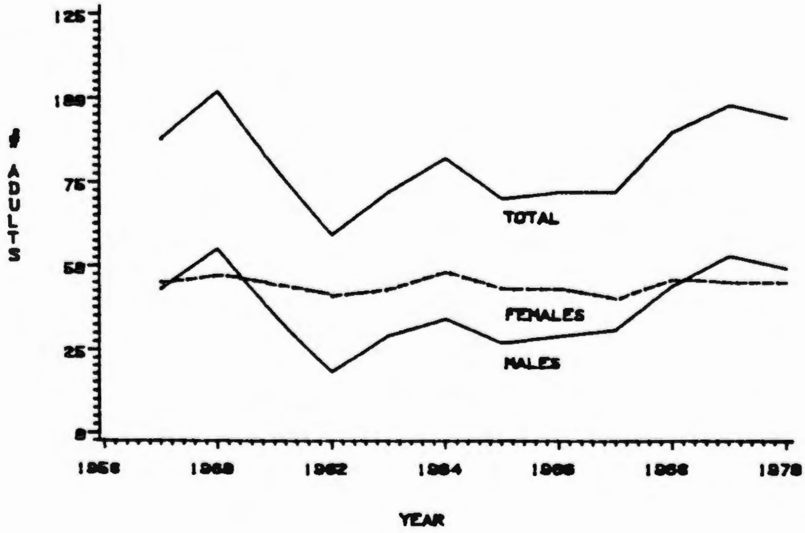


Fig. 3:3. Annual variations in densities of adults--total, males and females--among Yellowstone grizzlies (1959-70). Since density of adult females was so nearly constant, adult sex ratio varied in a pattern very similar to that for densities of adult males and total adults.

vs. total adult density can be used to estimate numbers of adult males and females during 1959-63. The equations used here are

$$\#AdM = -33.4 + 0.868*(\#Ad)$$

$$\#AdF = \#Ad - \#AdM \quad \text{(Fig. 3:3)}$$

The standard deviation for adult males was 4-fold larger than that for adult females during 1964-70 (10.4 vs. 2.6) and 5-fold larger during 1959-70 (11.5 vs. 2.3). Thus, for adults, just as for cubs, most variation in total density was to variation male density (males: r^2=96%, P:2t=0.0001; females: r^2=45%, P:2t=0.02).

Although the regressions used to estimate densities of male and female cubs or adults for years without data involve autocorrelation,

$$\#MC/\#C \text{ vs. } \#C \quad \text{and} \quad \#AdM/\#Ad \text{ vs. } \#Ad.$$

and may thus exaggerate correlation coefficients, this does not seem to distort the estimates themselves (see Chapter 9:I.C).

3:II. RELATIONSHIPS AMONG SIMPLE PARAMETERS

During each year t, reproduction is measured as the density of cubs known to have been produced then--an index of natality. Cub density in year t is, in turn, a function of several component parameters, as shown in Fig. 3:4. The most immediate are organized below by order of increasing influence or sequentially.

A) Mean cub litter size in year t.

B) Density of litters born in year t.

   1) Density of adult females in the population in year t.

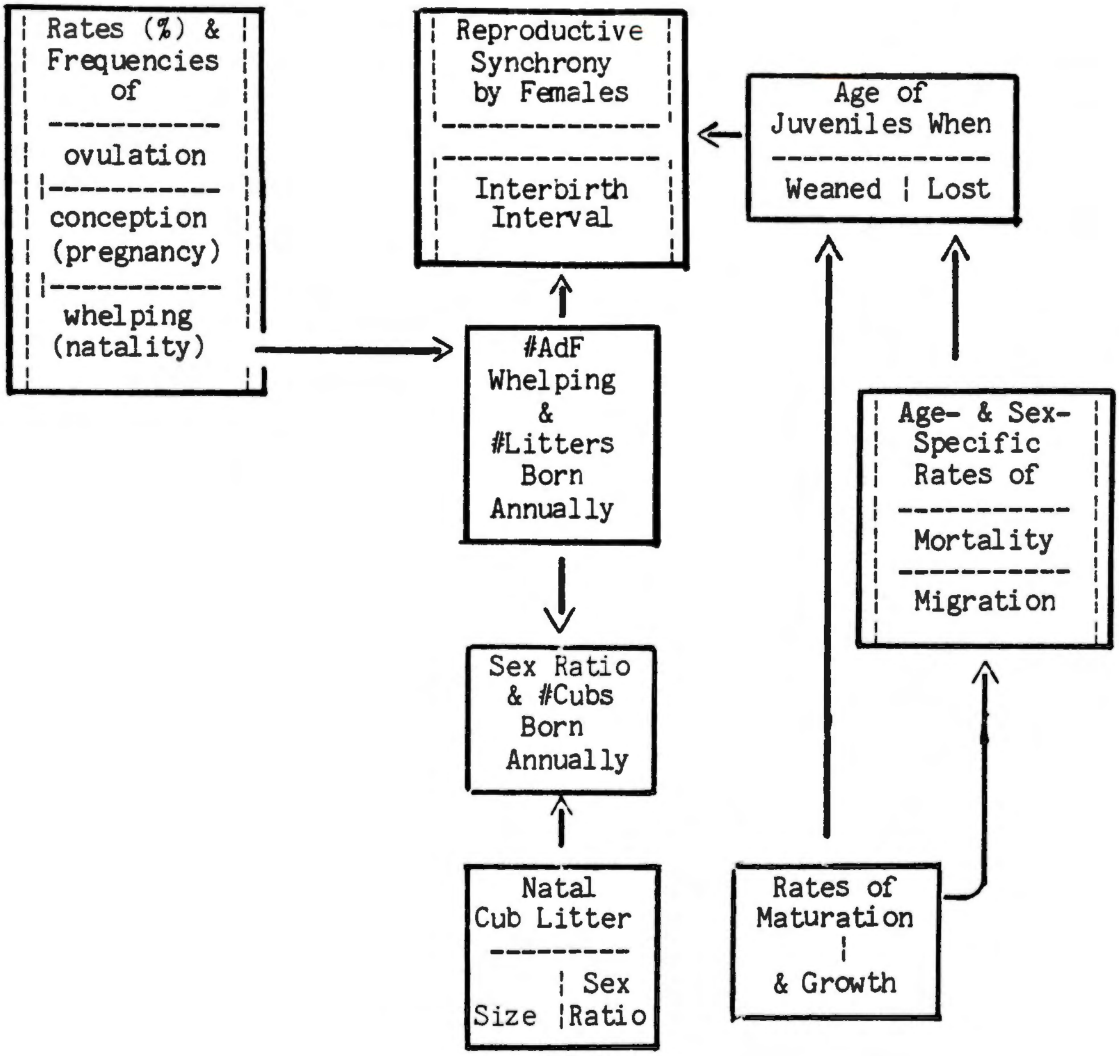


Fig. 3:4. Qualitative interrelationships among parameters of reproduction and recruitment.

    a) Density of female cubs born in each cohort during or prior to year t-G (G = generation length).
    b) Rate of maturation by those females to adulthood.
    c) Net recruitment rate for those females (due either to survival or immigration) during maturation.
    d) Net recruitment rate of these females as adults.

2) Proportion of adult females whelping in year t (whelping rate).
    a) How recently each last bore a litter.
    b) Length of her interbirth interval.

Each of the reproductive parameters was independently quantitatively evaluated by Stringham (in prep.); that includes consideration of how a female's age, maturity, and parity, affect her productivity and fecundity. Then, quantitative interrelationships among the reproductive parameters were analyzed. This built upon the earlier work by Stringham (1980) and Bunnell & Tait (1981).

3:III. COMPOUND INDICES

3:III.A. Productivity and Fecundity

Analysis and modeling of population dynamics and ecology is facilitiated if one considers responses by the reproductive parameters not only individually, but also in combination. Dividing cub litter size by interbirth interval (C/L/IBI) combines these 2 parameters to yield mean number of cubs produced per dam per year; that is often termed "productivity" (Pr). Cub sex ratio is incorporated by multiplying percent female cubs (%FC) against productivity, yielding a figure for per capita" fecundity" (Fc).

$$Fc = (\%FC)*(C/L/IBI) = (\#Daughters/dam/year)$$

The mean per capita fecundity calculated here for each species and population takes into account species-typical mean sex ratios for cubs, but not population-typical means. Except for Yellowstone grizzlies, it is only for the pooled data on each separate species that cub sex ratio sample size is large enough to be reliable. The species-typical means are about 45% daughters for both grizzly/brown and black bears, compared to about 50% for polar bears (Stringham, in prep.).

3:III.B. Reproductive Vigor and Population Growth Rate

The combined effects of fecundity and generation length, and thus the net effect of reproductive rate on population growth rate, is assessed by calculating the "reproductive vigor index." That is done by calculating the dominant eigenvalue of a Leslie Projection Matrix. The RVI is thus equivalent to the potential density independent rate of growth for a population whose age-sex structure and rates of reproduction and recruitment are stable (Appendix C). The dominant eigenvalue of a Leslie Matrix, and thus the RVI, is a multiplier. For instance, an eigenvalue of 1.10 indicates that population size is 1.10-fold as large in year t+1 as in year t. This can also be expressed as a growth rate of +10% per year; for simplicity, that is the form reproductive index values are given in this dissertation. Similarly, an eigenvalue of 0.93 is expressed as -7%.

Differences among species or populations in the reproductive vigor index reflect only corresponding differences in reproductive parameters. If infrastructural data were adequate for species-or population- differences in recruitment rates to also be taken into account, along with differences in reproduction, the dominant eigenvalue would represent "demographic vigor" [Caughley 1977]), rather than just reproductive vigor. But in lieu of data on differences in recruitment rates, the same recruitment schedule is used here for all populations and species. That schedule is the most reliable approximation available for female grizzlies, that presented by J. Craighead et al. (1974: Table 9), based on average size of each age-sex class over a 9 year period. (Details about the calculations are provided in Appendix C). Note that the fecundity value given for each population is a mean, averaged across all ages. By contrast, calculation of reproductive vigor was based on estimates of age-specific fecundities for each population.

PART II: RESPONSES TO ENVIRONMENTAL FACTORS

CHAPTER 4

INDICES OF FOOD SUPPLY, CLIMATE, AND NUTRIENT-ENERGY BALANCE

This chapter begins by discussing quantitative models and defining key terms. Various indices for food supply, climate, and nutrient-energy balance are examined. These serve as the basis for analyses in Chapter 5 of how these factors affect dynamics of bear populations.

4:I. QUANTITATIVE MODELS

As shall be detailed in the next 2 chapters, several studies have provided evidence for bears of positive correlations between rates of reproduction and recruitment vs. food supply or nutrient-energy balance. Attempts by the investigators to model those relationships have generally been limited to comparisons between years or populations with (a) low vs. medium vs. high body weights of mother bears or their cubs, or (b) scarce vs. abundant food, although Jonkel & Cowan (1971) did use 6 abundance ranks for food. Data has usually been inadequate for derivation of more precise "ratio" scale quantitative models, except in the cases of Jonkel & Cowan (1971), Rogers (1976, 1977, 1983), and Eiler (1981). Although even those authors did not use their data to derive regression models, some of it is presented in sufficient detail for the reviewer to do so (see Chapter 5:II and III).

One would expect most parameters of reproduction or recruitment to be related to nutrient-energy balance more-or-less sigmoidally (Fig. 4:1). This is apparent only if one considers responses to nutrient-energy balance over the full range of balances, from lowest to highest: (1) It is to be expected that below some minimum threshold of nutrient-energy balance, females cannot produce live young. (2) At a somewhat higher threshold, females may be able to reproduce, but the lower pre- and/or postnatal condition of the dam may well correspondingly impair nutrient-energy balance of the offspring so seriously that they do not survive. (3) Even better nutrient-energy balances of a dam and her offspring should improve offspring survivorship and their eventual success in competing for resources. (4) However, there may be an upper limit to the nutrient-energy balance that can be achieved under even the best of conditions; and there will certainly be a ceiling to survival even with optimal nutrient-energy balance.

Whether the sigmoid is linear or curvilinear between the lower and upper thresholds cannot yet be predicted a priori. Some of the parameters may be strictly linear functions of nutrient-energy balance between those thresholds. Others may rise from the lower limit reverse asymptotically, and/or approach the upper limit asymptotically. Furthermore, unless one has data on the parameter of reproduction or recruitment over the full range of possible nutrient-energy balances (NEB), one may be able to discern the function's shape over only that partial range, and not be able to

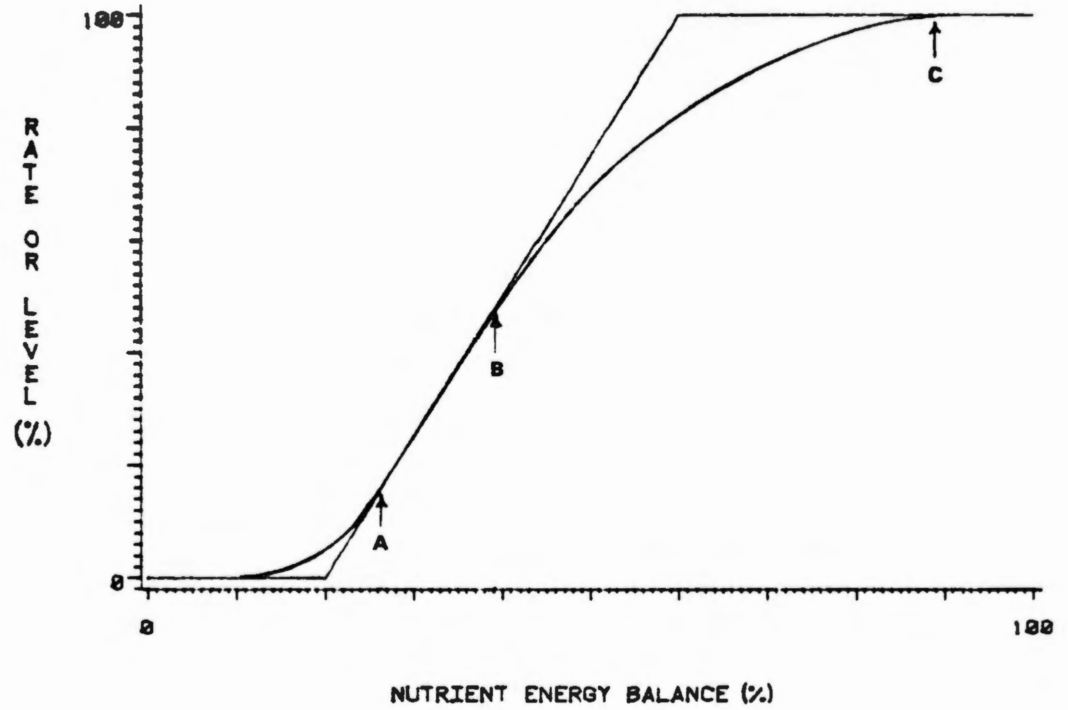


Fig. 4:1. Thresholds and functional relationships between rates or levels of reproduction and recruitment vs. nutrient-energy balance (schematic). Nutrient-energy balance (NEB) is scaled from 0% to 100% of the optimum that an animal can attain. Intermediate values are not labeled because each parameter of reproduction or recruitment might have different lower and upper threshold values of NEB. Rates (e.g., of whelping or survival) are scaled from 0-100% of the range of levels known or thought to occur (e.g., 0-100% of the maximum observed density of cubs in YNP: 40). Arrows indicate points above or below which lack of data could prevent one from (a) discriminating whether the relationship is sigmoid, logarithmic, or linear, or at least from (b) fitting a curve which describes the full complexity of the relationship (see text).

reliably extrapolate beyond it, or to interpolate. For example, apparent shapes for selected ranges of a monotonic sigmoid curve are given in Fig. 4:1: (a) If NEB < A, simple exponential curve; (b) if A < NEB < B, linear; (c)if B < NEB < C, logarithmic. Even where the proper form of the curve over the full range of nutrient-energy balances can be inferred, one may not be able to fit it to the data by regression if the data are available over too narrow a range of nutrient-energy balances; then, use of a simpler approximation curve may be unavoidable. So the reader is cautioned against extrapolating forms of the curves given here without taking into account that they may be only local approximations. Theoretically derived curves which can be extrapolated are discussed in Chapter 13.

In some, but not all cases, the upper and lower limits for a parameter of reproduction or recruitment can be inferred a priori. Rates of whelping, survival, and most other parameters cannot fall below 0% or rise above 100%. An exception is the rate of recruitment; it can exceed 100% since it can be affected by immigration as well as survival. The level of reproduction and survival cannot fall below 0. By contrast, litter size cannot fall below 1.0 C/L since without at least 1 cub there would be no litter. So too, interbirth interval cannot be shorter than about 1 year, since ovulation and impregnation occur during the spring-autumn period of one year and cubs are born during the following winter or early spring (see Stringham, in prep., for a review of data on dates of mating and parturition). If cub sex ratio responds to nutrient-energy balance of the dam, limits to responsiveness might begin either at or above 0% males and end at or below 100% males. One must consult data to obtain further detail about relationships between parameters of reproduction and recruitment vs. nutrient-energy balance and food supply.

The quantitative models used here were derived from 2 perspectives. (1) Newly available data were used to expand upon comparisons among grizzly populations by Stringham (1980) and Bunnell & Tait (1981), in the way done for polar bear populations by Bunnell & Tait (1981). (2) Comparisons were made among years for (a) grizzlies in Yellowstone, and for (b) black bears in Montana, Minnesota, and the Great Smoky Mountains.

To date, the YNP grizzly population is the most thoroughly studied bear population in the world, with data collected more-or-less continuously for 24 years since 1959. Although members of the Craighead research team (e.g., J. Craighead et al. 1969, 1974, 1976; F. Craighead 1979) have long referred to evidence of apparent positive correlations between rates of reproduction and recruitment vs. food supply for this population, they have not published formal proof of that, or even data on year-to-year variations in either natural forage or manmade garbage, the 2 major food sources. Fortunately, however, indices are now available for roughly estimating annual variations in these food sources, and in climate, and thus in their combined impact on individual nutrient-energy balance. Derivation of these indices shall be described later in this chapter.

Relationships between population dynamics vs. food supply and other controlling factors for black bears have been documented most thoroughly in the Montana, Minnesota, and Smoky Mountains populations studied, respectively, by Jonkel & Cowan (1971), Rogers (1976, 1977, 1983, in prep.) and Eiler (1981).

4:II. BASIC CONCEPTS AND TERMINOLOGY

"Food supply" refers here to the amount of food potentially available to the bears in a given habitat. Only when it is expressed on a per bear or per unit bear-mass basis does "food supply" take into account the density of bears that must share the food, and thus some aspects of intraspecific competition and density dependence. But even then, it does not subtract for (a) food that cannot be harvested profitably, (b) that which is lost to competitors, weather damage, and spoilage, etc., or (c) that which is for some reason inaccessible to at least some of the bears. For instance, salmon in streams may be effectively inaccessible to those individuals without sufficient skill to catch the fish. By contrast, subtraction for all of those factors is encompassed within the concept of food "availability."

Food availability is, in turn, a major determinant of food intake and thus of individual "nutrient-energy balance"--the balance between per capita income minus expenditures, between amounts of nutrients and energy consumed by each bear minus its expenditures for reproduction, growth, and maintenance (foraging, locomotion, thermoregulation, etc.). Weather, for instance, can affect amounts of hard mast (e.g., pine nuts or acorns) and berries (soft mast) that grow, as well as energy requirements of bears for thermoregulation (Figs. 4:2 and 4:3).

"Weather" refers here to short-term variations in temperature, precipitation. humidity, etc.; "climate" refers to long-term (e.g., annual) norms.

4:III. INDICES

Analyses for bears of relationships between reproduction and recruitment vs. food supply and nutrient-energy balance typically rest not on actual data for those controlling factors, but on surrogate indices. Only a few investigators have actually measured food supply, as detailed below, and apparently none has directly measured nutrient-energy balance.

(1) Stirling et al. (1975, 1976) and Stirling & Smith (1976) have quantitative data on abundance and availability of seals which are the main prey of a polar bear population in the Eastern Beaufort Sea. (2) Eiler (1981) presents weight data for amounts of hard mast (primarily acorns), but not for other foods, per unit area in the Great Smoky Mountains, at the border of Tennessee and North Carolina. (3) Hatler (1967), Collins (1974), and Rogers (1976, 1977, 1983, in prep.) simply categorized amounts of berries or hard mast as "scarce" vs. "abundant." To permit correlation tests on Rogers's data, each category was treated as a dummy variable and given a score of -5 or +5, respectively. Because the range of variation could exceed an

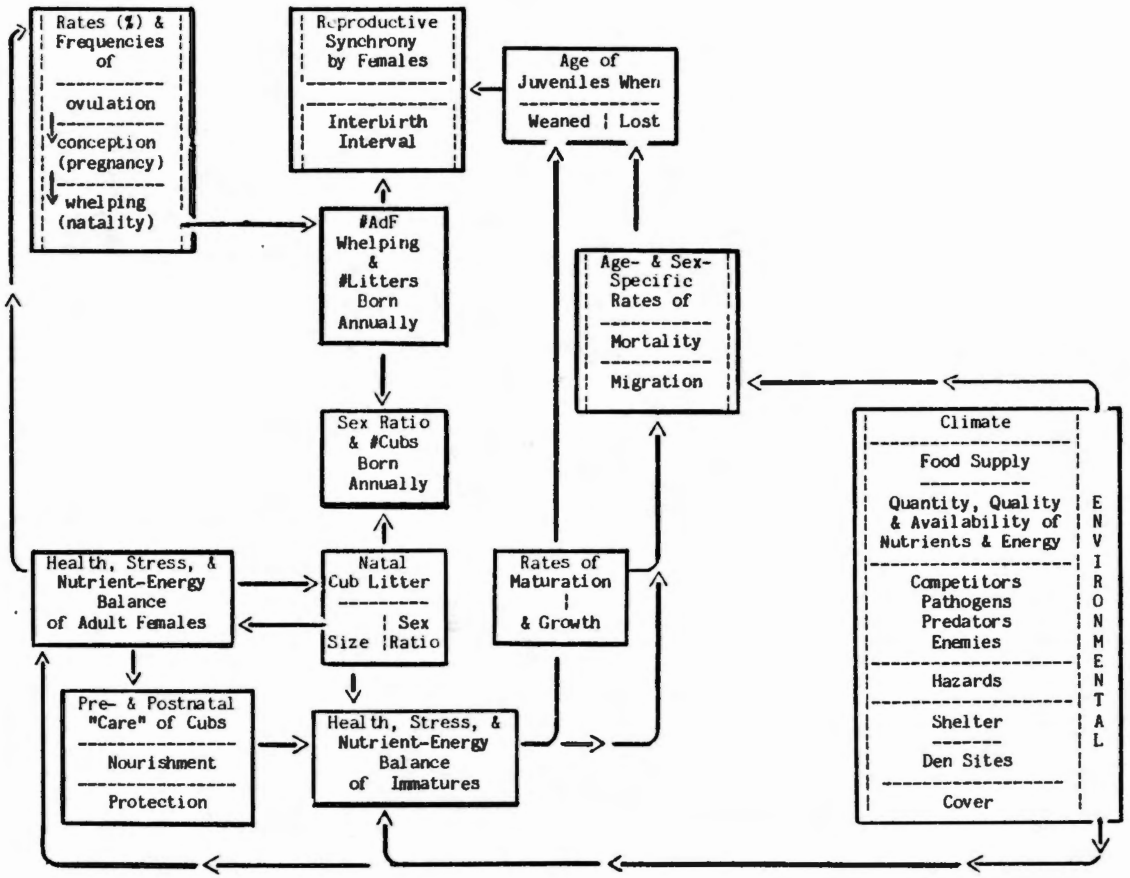


Fig. 4:2. Environmental influences on reproduction, survival, and migration within a bear population.

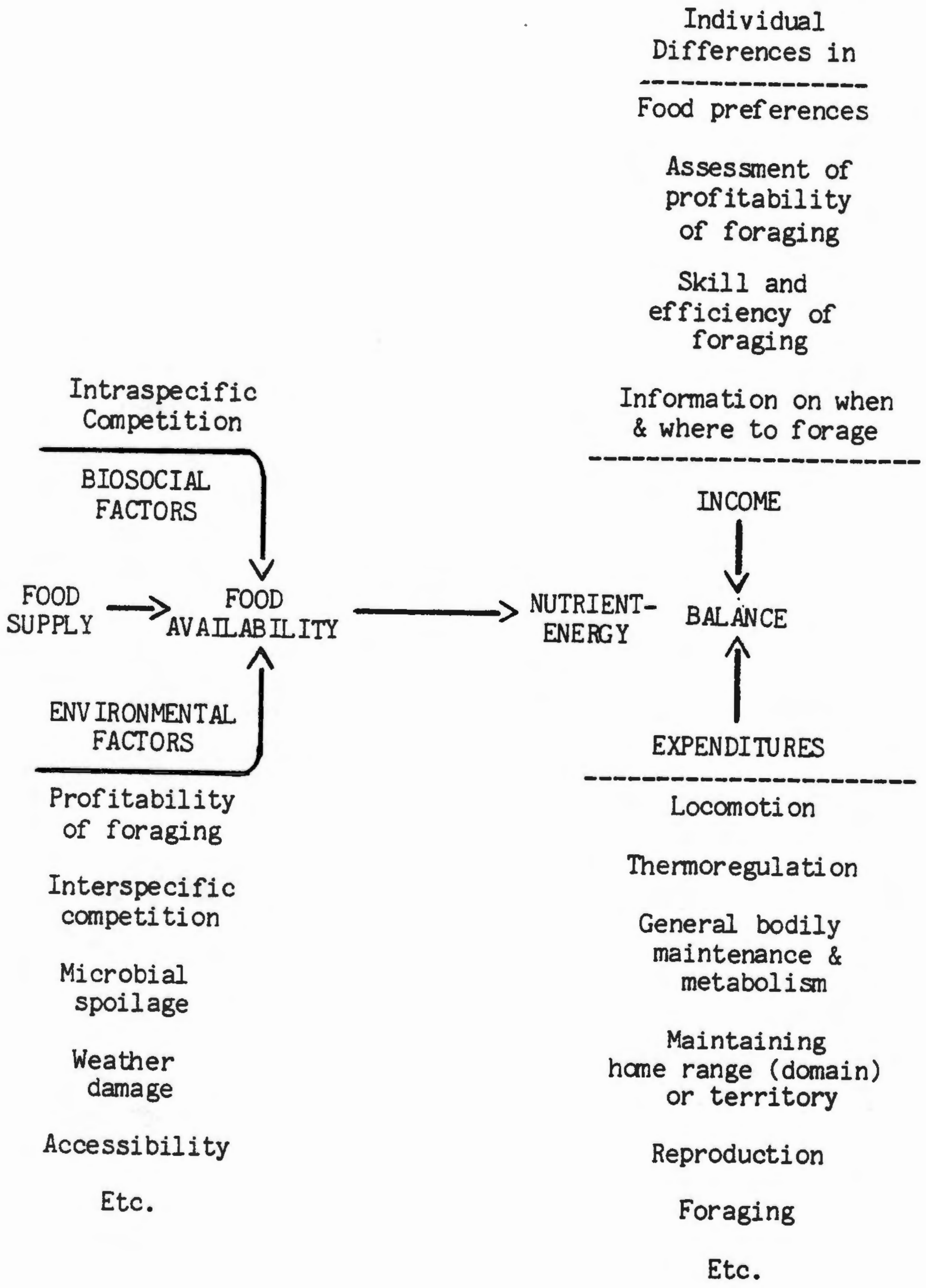


Fig. 4:3. Factors govening nutrient-energy balance, income, and expenditure.

order of magnitude (Rogers, pers. comm.), even dichotomous categorization of food as scarce vs. abundant provided considerable insight. Jonkel & Cowan (1971) instead distinguished 6 categories of food abundance; here, each was given a consecutive numerical scrore: very scarce (1), scarce (2), few (3), common (4), abundant (5), and very abundant (6), at each altitudinal zone. Then the scores for all 5 altitudinal zones were summed to give an overall annual score. Even such imprecise quantitative indices facilitate comparison of the findings on annual variations <u>within</u> habitats by those and other investigators.

By contrast, descriptions of food supplies as <u>typically</u> abundant or scarce in any given habitat provide much less basis for direct comparison <u>among</u> habitats. For example, what Rogers (1976, 1977) regarded as "abundant" might have encompassed all of the categories of "common" to "very abundant" distinguished by Jonkel & Cowan (1971). Furthermore, unless the same scale of abundance is applied in all habitats, a given level might be judged "abundant" in those habitats where it is above the local average, yet judged "scarce" in those other habitats where it is below the local average.

4:III.A. <u>Body Size and Weight</u>

It is partly in recognition of this problem that estimates of food supply, or implicitly nutrient-energy balance, are commonly linked to or based upon age-specific body size. It is explicitly or implicitly assumed that body size/weight/mass is directly proportional to individual nutrient-energy balance and to total food supply for the population. That has been well documented for other mammals (see Stringham, in prep.). The strongest evidence for this in bears comes from comparisons of wild bears subsisting primarily on natural foods vs. wild or captive bears receiving substantial amounts of manmade foods (Rausch 1961; Rogers 1976, 1977, in press; Russell et al. 1979; Eiler 1981).

Rausch (1961) compared growth rates for captive vs. wild black bears from south-central Alaska. The captives grew and apparently matured faster than the wild bears. Rausch attributed this to the facts that (a) the captives had a richer diet than was typical for wild bears in Alaska, and (b) captives hibernated less, and thus fed during a longer period each year. His data showed a 2-fold difference in sizes of captive vs. wild cubs 6 to 9 months old. By contrast, Rogers' (1976) data on Minnesota black bear cubs showed 2- to 5-fold differences. (Size differences for older bears were not given).

Among wild black bears in the Great Smoky Mountains, both males and females with ready access to garbage and handouts from people grow faster and attain higher mean adult weights than those subsisting primarily on natural forage (Eiler 1981). Similarly, Russell et al. (1979) reported that supplemental feeding on manmade food elevates physical condition of grizzly bears in Jasper National Park in Canada.

4:III.B. Latitude and Habitat Type

According to Harestad & Bunnell (1978), latitude is a good surrogate index for primary productivity of a habitat, as evidenced in part by the fact that home ranges of various mammalian species are positively correlated with latitude, irregardless of their body size or trophic proclivity. Another aspect of this is the positive correlation between latitude vs. length of the winter season when snow and other factors seriously reduce availability of nutritious food and elevate energetic costs of thermoregulation and locomotion--i.e., length of the season when bears fast in their hibernation dens.

Data (Table 4:1) are available from too few grizzly populations to support more than a preliminary test of whether either home range size or population density is correlated with latitude in this species. Such tests are complicated by intervening effects by habitat type.

For inland populations, latitude accounts for 40% (P:1t = 0.13, n=5) and 25% (P:1t = 0.16, n=6) of variance in (the log of) home range sizes for males and females respectively (primarily adults). When data from the coastal population at Chignik-Black Lakes are also included, latitude and habitat type together account for 42% and 40% of the variance in home range sizes (P:1t > 0.17). So this is at best weak substantiation for the hypothesis that home range size is positively correlated with latitude. Those tests did not include data from Kodiak Island. Range sizes documented there are apparently just seasonal, representating only the period while the bears aggregate

Table 4:1. Population density and home range size relative to latitude of the habitat for grizzly populations.

Habitat Type & Population	Latitude (°N)	Population Density (N/1000 km²)	Home Range Size (km²) Males	Females	M/F
COASTAL					
Kodiak Island, Karluk Lake (Troyer & Hensel 1964)	57.5	625	24 (7)	11 (23)	2.1
Chignik-Black Lakes (Glenn 1975; Glenn & Miller 1980)	56	67[1]	269 (4)	293 (30)	0.9
Mean	—	—	146	152	1.5
INLAND					
Eastern Brooks Range (Reynolds 1976)	69	4	--	--	--
Western Brooks Range (Reynolds 1980, in press)	69	8	1350 (8)	344 (18)	3.9
Northwest Territories (Miller et al. 1980)	65	12	--	265	--
Northern Yukon Territory (Pearson 1976)	69	--	414 (9)	73 (12)	5.7
Southwestern Yukon Territory (Pearson 1975)	61	37	287 (5)	86 (8)	3.3

Table 4:1. (Continued)

Habitat Type & Population	Latitude (°N)	Population Density (N/1000 km^2)	Home Range Size (km^2)		
			Males	Females	M/F
<u>INLAND</u>					
Montana Rockwell et al. 1978	49	--	513 (3)	104 (1)	4.9
Yellowstone National Park (J. Craighead et al., 1974, 1976)	45	71	161 (6)	73 (14)	2.2
Mean	—	—	582	193	3.6
<u>MEAN</u>			<u>473</u>	<u>184</u>	<u>3.1</u>

* After Stringham (1980: Table 2).

[1] Preliminary estimate.

near Karluk Lake to catch salmon, and are probably much smaller than the annual home ranges.

Among the 7 grizzly populations for which we have home range size data, the average size for males was 3-fold as large as that for females. The lowest difference in home range sizes for males vs. females was at Chignik-Black Lakes were small sample size may have resulted in underestimation of home range size for males, and where disturbance by hunters may have greatly restricted area used by adult males (Glenn & Miller 1980).

At 4 inland habitats above 60 degrees north latitude, average (unweighted) density was 15 bears/1000 km^2 compared to 346 bears/1000 km^2 in 2 coastal Alaskan populations (56-58 degrees north) and 71/1000 km^2 in YNP (45 degrees north). Latitude accounts for 96% of the variation in density among the 5 inland populations (Fig. 4:4). When the coastal population at Chignik-Black Lakes is also taken into account, r^2 drops to 87% for latitude alone, but is 97% for latitude and habitat type together. The second coastal population, from near Karluk Lake on Kodiak Island, supposedly had a density of 625/1000 km^2, which is about 10-fold as high as that recorded in any other grizzly population. Again, this was apparently just a seasonal concentration near Karluk Lake and may not be typical year around. (Even for black bears, density seldom exceeds 500 bears/1000 km^2, and the mean is close to 100/1000 km^2, Stringham, in prep). Consequently, latitude and habitat type (coastal vs. inland) together account for only 48% of the total variance in densities among all 7 of those

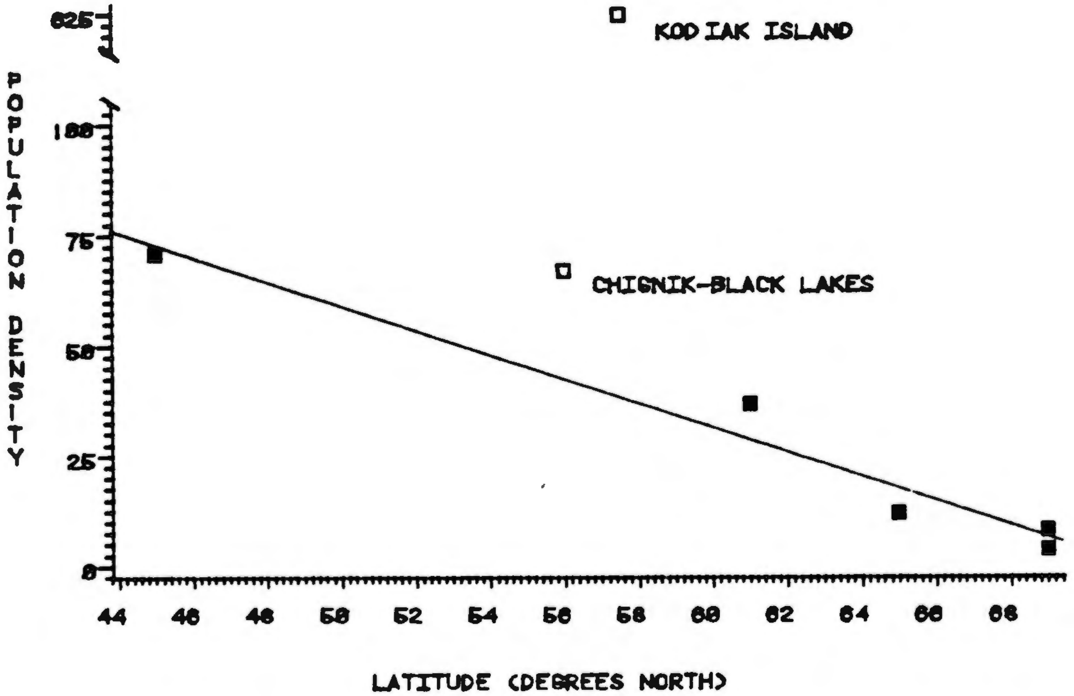


Fig. 4:4. Density of grizzly bear populations (bears/1000 km^2) regressed on approximate mid-latitude of the habitat. The regression line shown is for only the inland habitats (■). Data points for 2 coastal populations, at Chignik-Black Lakes and Kodiak Island, are also indicated (□). Density at Chignik-Black Lakes (CBL) is moderately higher than one would expect for an inland habitat at that latitude. But density at Kodiak Island is about 10-fold higher; this may be an artifact of censusing primarily where the bears aggregate to feed, particularly on salmon.

Inland only:	Den	=	197.3 - 2.77*Lat	r = 0.980, P:1t=0.001
Inland and CBL:	Den	=	218.4 - 3.05*Lat	r = 0.933, P:1t=0.003

inland and coastal grizzly populations (Fig. 4:4), including Kodiak Island. If density figures for the Karluk Lake region of Kodiak Island are indeed exaggerated, adjustment of them to represent the entire region used by the bears annually should raise the determination coefficient well above the current 48%. Results might also be improved if "density" could be expressed not just in terms of number of bears, but biomass of them; that could be calculated if the mean weight of bears in each age-sex class were known for each population.

If population density and home range size could be adjusted by subtraction of areas within each home range that are not habitat (e.g., barren rocky slopes), or which encompass mainly travel corridors, and the remaining area partitioned by habitat type or other controlling factors, correlations between home range size and density vs. latitude and habitat type might well be stronger. (These and other factors thought to govern home range size in bears are discussed in detail elsewhere). That suspicion is corroborated by the negative correlation between mean body weight of adult grizzlies vs. latitude, as detailed below.

Recall that. unless otherwise specified here, adults are at least 5 years old; however, in the next few paragraphs, 4-year-olds are also included as "adults" since that is how data for Glacier National Park was presented by Mundy & Flook (1973).

Considering only the 7 inland habitats, latitude accounts for 56% (P:1t<0.03) of variance in body weights for "adult" ($\geq$4-year-old) males and 68% (P:1t=0.01) of that for "adult" females (Fig. 4:5; Tables 4:2 and 4:3). Even within a given range of latitudes, body weights of "adults" are affected by topographic habitat type. Body weights of grizzlies tend to be higher in coastal habitats than in inland habitats for both "adult" females (T = 3.64, P:1t=0.004) and males (T = 2.37, P:1t<0.03). Together, latitude and habitat type (coastal vs. inland) account for 74% and 80%, respectively, of variance in body weights of ≥4-year-old male and female grizzlies.

It can be hypothesized that the differences in body weights among latitudes and between coastal vs. inland habitat types are largely attributable to differences in nutrient-energy balance of the bears. It is near the coasts where grizzlies most readily obtain salmon, and along the shoreline where they can obtain marine carrion (e.g., dead cetacea or pinnipeds) or live invertebrates (e.g., molluscs). Furthermore, coasts tend to have milder climates. Availability of abundant manmade foods, usually in the form of garbage, presumably can also elevate body weight higher than might be expected from latitude and habitat type alone.

Some of the variation in body size as a function of latitude and habitat type is presumably due to direct facultative (epigenetic) responses to food supply and climate, and thus to nutrient-energy balance, such that bears with the highest nutrient-energy balance grow fastest and largest. However, there may also be evolutionary adjustments in the genetic "reaction range" for body size, such that in habitats where average nutrient-energy balance is typically lowest,

Fig. 4:5. Mean body weight (Kg) for sampled grizzlies ≥4 years old regressed on approximate mid-latitude of the habitat (see also Table 4:3). In each multiple regression equation given below, the coefficient for the habitat type term estimates the amount by which body weight of coastal grizzlies (◘) would exceed that of inland grizzlies (■) at the same latitude, as indicated by the arrows to the ◆ symbols.

Males: BW = 577 - 4.22*Lat - 68.2*Hab
r = 0.859, P:1t=0.01, 0.02, 0.02.

Females BW = 331 - 1.97*Lat - 48.3*Hab
r = 0.894, P:1t=0.004, 0.02 0.005.

The first significance level for each plot is that for the overall equation; the second and third are, respectively, for the latitude and habitat type terms.

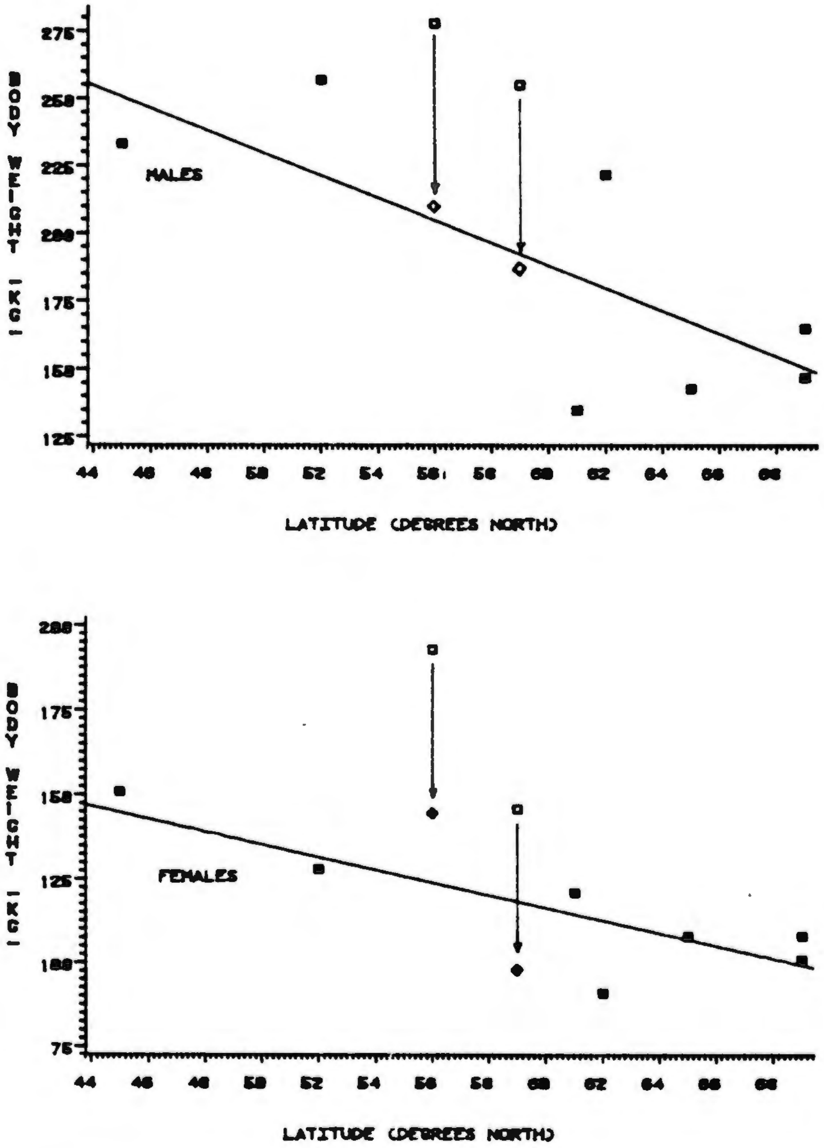


Fig. 4:5. (Continued)

Table 4:2. Age- and sex-specific body weights (Kg) for grizzly bears in North America.*

Sex, Habitat Type, and Population	Latitude (°N)	Age-Class Cubs	1 Year	2 Years	3 Years	4 Years	>4 Years	>5 Years
MALES Coastal								
Admiralty Island[1]	59	27 (3)	71 (3)	80 (2)	80 (2)	---	255 (4) 10.2yrs	255 (4) 10.2yrs
Chignik-Black[2] Lakes	56	20 (12)	65 (34)	125 (31)	170 (29)	200 (11)	278 (32) 6.5yrs	319 (21) 7.5yrs
Inland								
Eastern Brooks[3] Range	69	--	50 (2)	--	89 (2)	75 (2)	165 (40) 14.3yrs	170 (38) 14.8yrs
Western[4] Brooks Range	69	12 (6)	32 (3)	42 (2)	74 (6)	101 (5)	147 (40) 9.7yrs	153 (35) 10.4yrs
Northwest[5] Territories	65	30 (2)	63 (3)	98 (6)	99 (1)	110 (2)	143 (21) 11.6yrs	147 (19) 12.4yrs

Table 4:2. (Continued)

Sex, Habitat Type, and Population	Latitude (° N)	Age-Class						
		Cubs	1 Year	2 Years	3 Years	4 Years	>4 Years	>5 Years
MALES Inland								
Nelchina Basin[6]	62	5 (1)	--	79 (3)	120 (2)	150 (4)	222 (13) 8.0yrs	254 (9) 9.6yrs
Southwestern[7] Yukon Territory	61	12 (1)	40 (6)	45 (5)	73 (4)	70 (3)	135 (45) 10.3yrs	140 (42) 10.7yrs
Glacier National[8] Park, Canada	52	10 (1)	32 (4)	91 (1)	106 (2)	---	257 (4)	---
Yellowstone[9] National Park (1959-70)	45	32 (34)	68 (39)	111 (16)	125 (16)	153 (5)	233 (38)	245 (33)
Means (unwt.)[10]								
Coastal	58	24	68	102	125	200	266	287
Inland	60	17	48	78	98	110	186	186

Table 4:2. (Continued)

Sex, Habitat Type, and Population	Latitude (°N)	Age-Class						
		Cubs	1 Year	2 Years	3 Years	4 Years	>4 Years	>5 Years
<u>FEMALES</u> <u>Coastal</u>								
Admiralty Island[1]	59	31 (3)	--	64 (3)	91 (2)	91 (4)	146 (23) 10.5yrs	158 (19) 11.8yrs
Chignik-Black[2] Lakes	56	20 (11)	50 (26)	100 (18)	130 (3)	175 (20)	193 (83) 7.7yrs	198 (63) 8.7yrs
<u>Inland</u>								
Eastern[3] Brooks Range	69	--	43 (2)	57 (2)	73 (1)	85 (2)	101 (40) 11.3yrs	102 (38) 11.7yrs
Western[4] Brooks Range	69	13 (10)	32 (8)	50 (3)	63 (4)	72 (5)	108 (50) 12.3yrs	112 (45) 13.2yrs
Northwest[5] Territories	65	--	--	--	76 (2)	90 (3)	108 (31) 11.1yrs	110 (28) 11.8yrs

Table 4:2. (Continued)

Sex, Habitat Type, and Population	Latitude (°N)	Age-Class						
		Cubs	1 Year	2 Years	3 Years	4 Years	>4 Years	>5 Years
<u>FEMALES</u> <u>Inland</u>								
Nelchina Basin[6]	62	5 (1)	45 (2)	74 (3)	--	98 (2)	121 (13) 8.9yrs	125 (11) 9.7yrs
Southwestern[7] Yukon Territory	61	--	28 (1)	37 (2)	57 (5)	63 (3)	91 (24) 9.4yrs	95 (21) 10.6yrs
Glacier National[8] Park, Canada	52	--	--	--	113 (1)	--	128 (3)	---
Yellowstone[9] National Park	45	27 (17)	58 (19)	84 (22)	125 (7)	132 (4)	151 (76)	152 (72)
<u>Means (unwt.)</u>[10]								
<u>Coastal</u>	58	26	50	82	110	133	170	178
<u>Inland</u>	60	15	41	60	84	90	115	116

Table 4:2. (Continued)

* Values given are mean weight for each age class, sample size for weights (n), and mean age for sampled "adults."

[1] Wood (1975).

[2] Glenn (1980).

[3] Reynolds (1976).

[4] Reynolds (1981).

[5] Miller et al. (1981).

[6] Spracker et al. (1980).

[7] Pearson (1975).

[8] Mundy & Flook (1973). Data for $\geq$4-year-olds lumped by the authors.

[9] Craighead & Mitchell (1982). Weight data were used from the 1959-70 period, that is representing primarily the period prior to closure of the YNP garbage dumps (see Section III.C; Table 4:5), since that is also the period when most data on reproduction and recruitment were available. Had weight data strictly for the post-closure period (see Table 4:5) been used instead, the correlations with latitude would have been somewhat weaker.

[10] Since Glenn et al. (1980) provided only means, not the raw data, for age-classes up through age 4 years, one cannot calculate sample-size weighted means for coastal vs. inland habitats; even if one could, that would give the greatest emphasis to the individual populations where samples were largest. Use of unweighted means gives each population within a habitat type equal weight, irregardless of the number of bears in each that were weighed.

Table 4:3. Body weights for "adult" grizzlies correlated with habitat type and approximate mid-latitude of the habitat.*

Habitat Type & Age Class	Males	Females	Unweighted Mean for Both Sexes
<u>INLAND</u> <u>Wt. vs. Lat</u> [1]			
>4 years old (n=7)	-0.749 0.03	-0.826 0.01	-0.800 0.02
>5 years old [2] (n=6)	-0.699 0.04	-0.816 0.01	-0.757 0.03
<u>INLAND & COASTAL</u> <u>Wt. vs. Lat.</u>			
>4 years old (n=9)	-0.699 0.02	-0.600 0.04	-0.672 0.02
>5 years old (n=8)	-0.630 0.03	-0.565 0.55	-0.624 0.03
<u>Wt. vs. Lat.</u> <u>& Hab. Type</u> [3]			
>4 years old (n=9)	-0.860 0.01	-0.894 0.004	-0.899 0.03
>5 years old (n=8)	-0.828 0.02	-0.920 0.0005	-0.877 0.005

* Data from Table 4:2. Values given are r and P:1t, where the null hypothesis is that body weight is <u>not</u> highest where food supply and nutrient-energy balance are highest.

[1] Body weight linearly correlated with latitude.

[2] For Glacier National Park, Canada, data were lumped for all bears at least 4 years old, rather than on all at least 5 years old, as is conventional for other populations.

[3] Body weight linearly correlated with both latitude and habitat type.

bears tend to invest less in growth, even during temporary superabundances of food.

4:III.C. Garbage Supply in Yellowstone National Park

Particularly in habitats where natural foods provide little protein or fat, manmade garbage can be a crucially important supplemental source of those nutrients (J. Craighead et al. 1974, 1982; F. Craighead 1979; Rogers 1976; Eiler 1981; Pelton 1982). That was apparently true in YNP. Hence, analysis of the YNP data in Chapter 5 considers effects on population dynamics by variations in (indices for) supplies of both natural foods and garbage.

Inquiries with National Park Service officials at Yellowstone National Park indicate that records were kept on amount of garbage collected only during 1980. There was about 1 ton of "edible" garbage per 3000 visitors. Thus, assuming that the ratio of edible garbage per visitor was relatively stable during 1959-68, the number of people visiting YNP each year can be used as an index of garbage supply each year. An NPS official provided figures for annual visitation during 1895-1980, and for visitation during May-September of 1950-81. Corresponding estimates of edible garbage supply are given in Table 4:4.

Applicability of that garbage supply index to ecology of YNP grizzlies is readily demonstrable. Hornocker (1962: Fig. 2) identified June-September as the period when grizzlies made most use of the dumps. Counts were made on only a few days of each month. The

Table 4:4. Indices of food supply and nutrient-energy balance for Yellowstone grizzlies, 1959-81.

Year[1]	Natural[2] Food Supply	Garbage[3] Supply	Total[4] Food Supply	Supply[5] per Bear	Supply[6] per unit Bear Mass
Prenatal		----	----	----	----
Postnatal		----	----	----	----
Circumnatal	----	----	----	----	----
1959	(2)	463	581	3.77	2.73
1958		470	588	.	.
1958-59	118	466	584	.	.
1960	(-7)	470	58	0.34	0.23
1959		463	51	0.33	0.21
1959-60	-412	466	54	0.34	0.22
1961	(3)	497	674	4.06	3.08
1960		470	647	3.83	2.49
1960-61	177	484	660	3.94	2.76
1962	(-1)	610	551	3.56	3.05
1961		497	438	2.64	2.00
1961-62	-59	554	495	3.08	2.48
1963	(8)	607	1078	6.09	5.13
1962		610	1081	6.98	6.47
1962-63	471	608	1080	6.50	5.73
1964	(0)	627	627	3.39	2.66
1963		607	607	3.43	2.81
1963-64	0	617	617	3.41	2.73
1965	(2)	670	788	4.21	3.60
1964		627	745	4.03	3.02
1964-65	118	648	766	4.12	3.29
1966	(-4)	683	447	2.21	1.83
1965		670	434	2.32	1.86
1965-66	-237	676	441	2.27	1.85

Table 4:4. (Continued)

Year	Natural Food Supply	Garbage Supply	Total Food Supply	Supply per Bear	Supply per unit Bear Mass
Prenatal		----	----	----	----
Postnatal		----	----	----	----
Circumnatal	----	----	----	----	----
1967	(7)	713	1125	6.43	5.19
1966		683	1095	5.42	4.49
1966-67	412	698	1110	5.84	4.82
1968	(6)	720	1073	5.93	4.36
1967		713	1066	6.09	4.91
1967-68	353	717	1070	6.01	4.62
1969	(2)	.	.	.	.
1968		720	838	4.63	3.41
1968-69	118	.	.	.	.
1970	(0)	0	0	0	0
1969		.	.	.	.
1969-70	0	.	.	.	.
1970-71[7]	(-2)				
	-118	0	-118		
1971-72	(1)				
	59	0	59		
1972-73	(-7)				
	-413	0	-413		
1973-74	(-1)				
	-59	0	-59		
1974-75	(-12)				
	-707	0	-707		

Table 4:4. (Continued)

Year	Natural Food Supply	Garbage Supply	Total Food Supply	Supply per Bear	Supply per unit Bear Mass
Prenatal		----	----	----	----
Postnatal		----	----	----	----
Circumnatal	----	----	----	----	----
1975-76	(3) 177	0	177		
1976-77	(-4) -236	0	-236		
1977-78	(1) 59	0	59		
1978-79	(-5) -294	0	-294		
1979-80	(1) 59	0	59		
1980-81	(0) 0	0	0		

[1] The year in which each parameter of reproduction or recruitment was assessed (median age about 0.5 year) is considered to be the postnatal year. So information on possible controlling factors such as food supply is presented accordingly. Postnatal values of controlling factors are given first to facilitate comparison with corresponding values of the parameters of reproduction and recruitment. Thus, a garbage supply of 463 in 1959 is the postnatal supply for the 1959 birth cohort and prenatal for the 1960 birth cohort.

Table 4:4. (Continued)

[2] As detailed in the text, Picton's (1978) climate index for October-May of each year can also be used as an index for natural food supply (NFS) and nutrient-energy balance (NEB). Because cubs are usually born in late January to early February, the October-May period encompasses both pre- and postnatal time spans and is thus descried as being circumnatal. The original climate index value (e.g., 2 for 1959) is given in parentheses in the row for postnatal; then that value is scaled to units equivalent to those for garbage supply (NFS-NEB = CI*59) and given (e.g., 118 for 1959) below in the row for "circumnatal."

[3] Estimated number of tons of "edible" garbage potentially available to the Yellowstone grizzlies each year during May-September.

[4] TFS = NFS + GS.

[5] Supply per bear = TFS/N, where "N" is total population size for the year (see Table 3:5).

[6] Supply per unit bear mass = TFS/BM, where "BM" is calculated by multiplying average weight (mass) of bears in each age-sex class by number in the class, then summing, as explained in the text. Weight data are taken from Table 4:5. Figures used for immatures are those at the bottom of Table 4:5 for both sexes combined, during 1959-70. Those used for adults are separated by sex for the same period. Note that figures in Table 4:5 have been rounded off and are thus slightly less precise than those used in these calculations.

[7] For 1971-81, only climatic (natural food supply) index values are available, garbage supply in YNP apparently being near 0.

only date common to all 4 months is the 15th. Averaging data over the 3 years of his study, 1959-61, Hornocker estimated numbers of grizzlies visiting dumps on the 15th day of each month, from June through September. Regression of those estimates of grizzly density vs. the mean monthly supply of edible garbage (GS, in tons) yields the equation:

$$(\#\text{Grizzlies}) = -10.6 + 0.493*(\text{GS}) \qquad \text{Fig. 4:6}$$

($r = 0.988$, $P{:}1t = 0.001$). In other words, for every additional 2.03 tons of edible garbage each month during June-September, 1 more grizzly was known to have fed at the dumps each day. For a 31-day month, that would be roughly 131 pounds or 60 Kg of edible garbage per day per grizzly observed at the dumps.

No information is available on what portion of that was actually consumed by the grizzlies, rather than by competitors (e.g., black bears, rodents, or birds), or which was unobtainable for some other reason. Furthermore, number of grizzlies feeding at dumps may have exceeded the number actually seen. Total density of grizzlies counted during each of those 3 years averaged 163 bears in YNP; that corresponds to between 212 and 286 grizzlies in the entire Yellowstone Ecosystem, according to the estimates of censusing efficiency by J. Craighead et al. (1974: 77%) and McCullough (1981: 57%), respectively (see Chapter 12:I.A.1). But even if each grizzly feeding at dumps actually obtained only a fraction of the 60 Kg per day of garbage potentially available to it, the importance of garbage to the diet of grizzlies is attested to by the fact that 98% of variation of grizzly

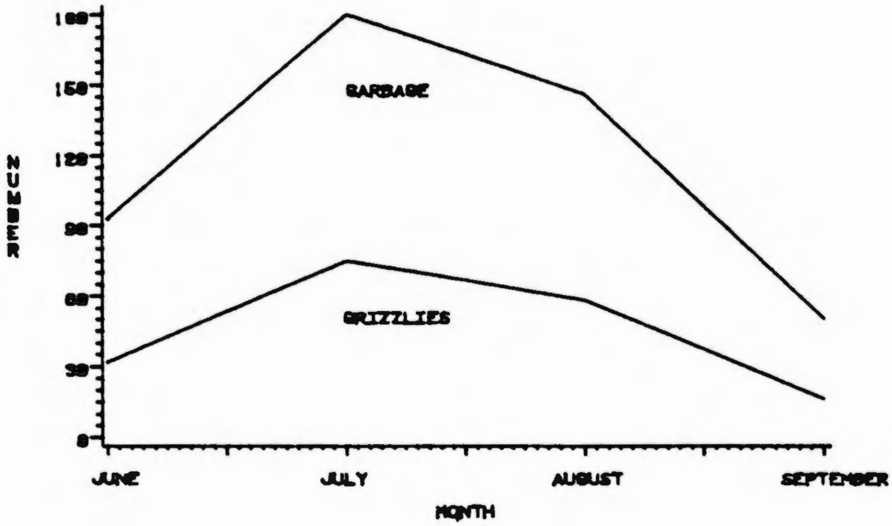


Fig. 4:6. Number of grizzlies using Trout Creek dump on the 15th day of each month (June - Sept) during 1959-61, regressed on mean garbage supply index for that month in Yellowstone National Park.

density at dumps during mid-June through mid-September was statistically accounted for by variations in garbage supply. Thus, the garbage supply index should also provide a reasonably good basis for estimating how variations in garbage supply affected rates of reproduction and recruitment.

This is not, however, to suggest that garbage supply was always the dominant factor governing grizzly density at the dumps. (1) With mean values based on only 1 date per month for mid-June to mid-September over 3 years, the figure 98% of variance accounted for by garbage supply could be exaggerated. (2) Hornocker notes that availability of natural foods and weather both affected how soon grizzlies dispersed from the dumps after mid-September. During an autumn when whitebark pine seed cones were particularly abundant, and in another when snow fell early, dispersal from dumps was earlier than in other years. In all 3 years of Hornocker's study, dispersal began and ended while there were still large quantities of manmade foods available at the dumps.

Visitor numbers can be used to estimate garbage supply only up until 1968, since it was then that dump closure began to substantially reduce amounts of garbage available to the bears. I have not been able to obtain any estimates of how rapidly garbage supply diminished. But data for litter size vs. climate index show that the slow rise in litter sizes during the pre-closure period 1959-68, was followed by a rapid decline over the next 2 years (Fig. 4:7). Litter size in 1971 was comparable to that in 1970, suggesting that by 1970, little

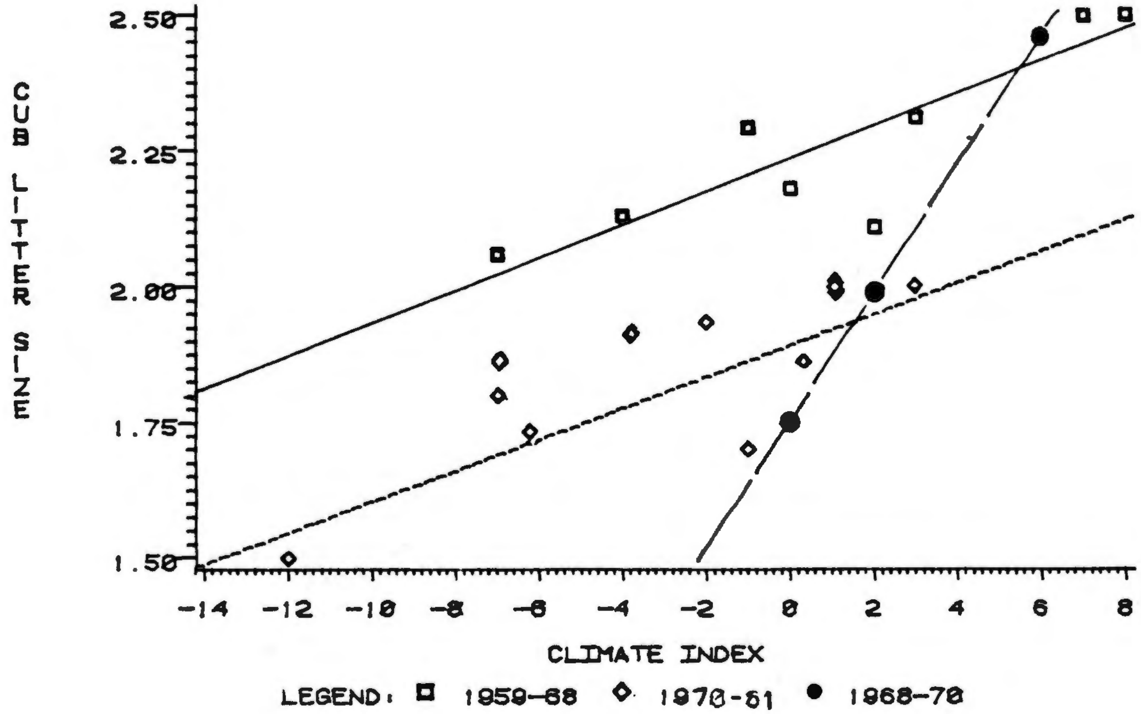


Fig. 4:7. Cub litter size regressed on climate, based on Picton's (1978) index of winter severity for Yellowstone National Park. The upper and lower lines represent periods before vs. after dump closure began, respectively. The third line (●) represents the period while dump closure was underway (see text for details and equations).

garbage was left available to adult females within YNP, despite the fact that closure of the Trout Creek dump was not completed until sometime that year. Furthermore, some garbage was available at the West Yellowstone dump throughout 1970, and at the small municipal dumps at Gardiner and Cooke City during subsequent years (Cole 1971a,b, 1976; Schullery 1980; Knight et al. 1981). Because I have no way of estimating how much garbage has been available from those peripheral sources, the garbage supply index used here applies only to garbage available from the YNP dumps themselves, which I estimate to have been near 0 since 1970. During 1969 garbage supply was intermediate; but no firm estimate can be made as to its level; so it is treated as a "missing value" for now. If an when more data can be obtained on garbage supply after 1968, these estimates may need revision. But that should necessitate only minor changes in the results obtained here.

4:III.D. An Index for Natural Food Supply, Nutrient-Energy Costs of Living, and Climate for YNP Grizzlies

There is little doubt but that climatic parameters, for instance temperature and precipitation, affect both nutrient-energy costs of living and availability of natural foods (including carrion, in the case of food for bears). That is probably why the climate index derived by Picton (1978, 1979, in press) is a reasonably good predictor of mean annual litter size for Yellowstone grizzlies, survivorship of mule deer fawns (*Odocoileus hemionus*, Picton 1978, 1979), and reproductive rate in Yellowstone wapiti (Houston 1982).

Picton derived the index of winter-spring climate from monthly and long-term means for temperature and precipitation at the Mammoth weather station in YNP. The value for each parameter each month from September or October to May each year was given a score according to how many standard deviations it was from the 1958/59 - 1975/76 mean. Variations within 1 SD were given a score of +1 or -1; those greater than 1 SD were given a score of +2 or -2. Then the number of deviations for temperature and precipitation were summed. The September-May climate index for each winter accounts for 43% (P:2t < 0.01) of the variance in cub litter sizes for the following summer during the 18 year period 1959-76 (Picton 1978, in press).

4:III.E. Total Food Supply and Nutrient-Energy Balance Indices for YNP Grizzlies

An index for annual variations in total (natural plus manmade) food supply and nutrient-energy balance was obtained here by combining the garbage supply and climate indices. The first step in combining them was to rescale climate index values into units equivalent to those for garbage supply. That was begun by doing a multiple regression on litter size vs. climate index for 1959-81, excluding the years 1969-71 while dump closure was in progress, using the October-May climate index (Fig. 4:7):

$$1959\text{-}81: \quad C/L = 2.19 + 0.0294{*}CI - 0.260{*}DC + 0.000250{*}(CI{*}DC)$$

(R = 0.843, P:1t < 0.0001). The slope of the equation, the CI term, represents the amount of change in litter size per unit change in climate, independently of any simultaneous decline induced by dump closure. Slope was not affected by closure (P:2t > 0.99), judging from the interaction or covariance term (CI*DC) of the multiple regression. Hence, the relationship between litter size vs. climate is represented by 2 parallel lines in Fig. 4:7, the upper line for the pre-closure period (1959-68), the lower for the post-closure period (1972-81). The litter size decline induced by dump closure (DC) independently of climatic change, is approximated by the DC term (0.260 C/L), and appears in Fig. 4:7 as the vertical separation between the before vs. after lines. (See Chapter 5:II.A,. and Stringham, in prep., for further details.)

<u>Note:</u> Calculations for the total food supply and nutrient-energy balance index were made prior to obtaining some of the most recent data. The slope and dump closure terms obtained then were 0.0290 and 0.30, respectively--a negligible difference from the 0.0294 and 0.26 vaules given above. So results obtained with the preliminary values should differ negligibly from those which would be obtained if one revised the regression and correlation tests with the new values. Hence, such revision was deemed unnecessary and was not done.

A 0.30 C/L decline in litter size represents the impact from eliminating an average of about 607 tons of edible garbage per summer potentially available for consumption by the grizzlies. It is as much change in litter size as would have been induced by a change in climate of about 10.34 units (= 0.30/0.029). So, to convert climate index values (CI) into the units equivalent to those for garbage supply (GS), one can use the formula:

NFS-NEB = CI*(59) = CI*(0.029/0.30)*(607)

where NFS-NEB denotes an index for natural food supply and for nutrient-energy balance. Thus, for 1959 when CI = 2, NFS-NEB = (2)*(59) = 118.

To calculate the total food supply and nutrient-energy balance index, the rescaled NFS-NEB (climate) index is then added to the garbage supply index:

TFS-NEB = GS + NFS-NEB

For 1959, TFS-NEB = 463 + 118 = 581 (Table 4:4,p.79).

Note that Picton's (1978) climate index was given on a standardized scale, where "0" is the mean. Thus, below-average values for CI and NFS-NEB are negative. Conseqently, once garbage became scarce, during 1970-81, 75% (8/12) of the TFS-NEB index values were also 0 or negative. Again, this implies that they were at or below average, <u>not</u> that food supply or nutrient-energy balance was 0 or negative.

The fact that units of the climate index can be converted into units equivalent to those for garbage supply does not suggest that the NFS-NEB index represents an equivalent weight of natural foods (e.g., 118 tons for 1959). Whether the weight of garbage was even proportional to the weight of natural foods would have depended on a number of factors, including nutritional content per unit weight of garbage vs. natural food of each kind, and variation in proportion of each kind. Recall that the NFS-NEB index might also incorporate some metabolic costs of thermoregulation during hibernation and perhaps of locomotion through snow.

Certainly, there is unlikely to be an exact relationship between the values for the TFS-NEB index vs. actual amounts of food (natural and manmade) or any actual measure of nutrient-energy balance (e.g., body weight or fat:lean ratio). However, it is not the exact values of the index which are important, but the relative values and the pattern of their variations from year to year; it is those variations which are expected to correspond, at least roughly, to variations in actual food supply and nutrient-energy balance. Unfortunately, without data on food supply and nutrient-energy balance per se, the strength of their correlations with the TFS-NEB index can only be inferred, in part from how well TFS-NEB predicts per capita rates of reproduction and recruitment, as well as densities of cubs and older recruits.

Even better approximations of mean individual nutrient-energy balance should be obtainable by calculating food supply per bear and especially per unit bear mass. Supply per bear is estimated by dividing the total food supply and nutrient-energy balance index with total population size for each year (TFS/N-NEB). Supply per unit bear mass is estimated by dividing with population biomass for each year (TFS/BM-NEB).

Biomass is estimated by multiplying number of grizzlies in each age-sex class with mean body mass (weight) for that class.

$$BM = [\#C*BM_c + \#Y*BM_y + \ldots + \#AdM*BM_m]$$

For example, there were 26 yearlings and 23 2-year-olds censused in 1959. Mean masses for those age-classes (1959-70) were 64.6 Kg and 95.2 Kg, respectively (J. Craighead & Mitchell 1982; see Table 4:5). So, total masses of yearlings and 2-year-olds were roughly 1680 Kg and 2190 Kg, respectively. Although yearlings outnumbered 2-year-olds, total mass of 2-year-olds was greater.

As noted earlier, data of J. Craighead et al. (1974) on density of grizzlies in each age-sex class lumped information on both sexes except for some cubs and for adults (Tables 3:2, p.29, and 3:6, p.34); so body mass values also had to be averaged for male and female juveniles. Likewise, body mass values were averaged for 3- and 4-year-old subadults, since density data on them was also lumped (Table 4:5).

Since weights are known only on average for 1959-70, rather than annually, all variation in estimated biomass each year is due to variation in density within each age-class; so in Chapter 8 regressions on density of adult males or any other <u>single</u> age-sex class are statistically equivalent to regressions on biomass of that age-sex class. Only if annual variations of age-sex class specific body weights were known would correlation coefficients for relationships with density of a class different from those with biomass of the class.

Table 4:5. Age- and sex-specific body weights (Kg) for Yellowstone grizzlies before vs. after completion of closure of garbage dumps within YNP.*

		Age-Class					
Sex	Period	Cubs	1-Year	2-Year	3-Year	4-Year	5-Year
Male	1959-70[1]	32 (34)	68 (39)	111 (16)	125 (16)	153 (5)	245 (33)
	1974-80[2]	33 (6)	68 (8)	101 (9)	125 (4)	135 (6)	183 (35)
	Difference	+3%	0	-9%	0	-12%	-25%
Female	1959-70	27 (17)	58 (19)	84 (22)	125 (7)	132 (4)	152 (72)
	1974-80	25 (3)	64 (5)	99 (4)	108 (2)	121 (5)	127 (23)
	Difference	-7%	+10%	+18%	-14%	-8%	-16%
Male & Female	1959-70[3]	30 (51)	65 (58)	95 (38)	125 (23)	144 (9)	181 (105)
	1974-80	30 (9)	66 (13)	100 (13)	119 (6)	129 (11)	171 (58)
	Difference	0	+2%	+5%	-5%	-10%	-6%

* Sample size in parentheses (n).

[1] Data from J. Craighead & Mitchell (1982:Table 25.1).

[2] Data from Knight et al. (1981:Tables 9 and 10).

[3] Sample-size weighted means.

When discussion is focused on only one of the indices for food supply and nutrient-energy balance (TFS-NEB, TFS/N-NEB, or TFS/BM-NEB), it shall be specified. But when discussion is general enough to apply to any of the indices, or to the phenomena indexed, the term "food supply and nutrient-energy balance" (FS-NEB) is used.

Recall that food supply and nutrient-energy balance data encompasses garbage supply during each summer (May-September). Supply during the summer when each cohort was conceived is termed the "prenatal" supply, whereas that following birth, when cubs were censused at an average age of about 0.5 year, is termed the "postnatal" supply. The average garbage supply for the pre- and postnatal years is termed the "circumnatal" supply. ("Circumnatal" is also sometimes used to designate both pre- and postnatal periods more loosely). By contrast, the NFS-NEB index encompasses climatic data during October-May. Because cubs typically implant (as blastocysts) in late November and are born in late January or early February (see J. Craighead et al. 1969), NFS-NEB (climatic) data encompasses a narrower portion of the circumnatal period than does the average garbage supply pre- and postnatally. Also, the NFS-NEB index is not separable into prenatal vs. postnatal periods in the way that data on garbage supply is. Thus, when for simplicity, an index for food supply and nutrient-energy balance is referred to as either "prenatal" or "postnatal," it encompasses prenatal or postnatal garbage supply, respectively, and circumnatal NFS-NEB (climate). "Circumnatal" food supply and nutrient-energy balance refers to average garbage supply pre- and postnatally, as well as circumnatal NFS-NEB (climate).

$$\text{TFS-NEB}_{\text{prenatal}} = \text{GS}_{\text{prenatal}} + \text{NFS-NEB}_{\text{circumnatal}}$$

$$\text{TFS-NEB}_{\text{postnatal}} = \text{GS}_{\text{postnatal}} + \text{NFS-NEB}_{\text{circumnatal}}$$

$$\text{TFS-NEB}_{\text{circumnatal}} = \text{GS}_{\text{circumnatal}} + \text{NFS-NEB}_{\text{circumnatal}}$$

(Table 4:4, p.73). Because these indices (TFS-NEB, TFS/N-NEB, TFS/BM-NEB) encompass both climatic and garbage supply indices, they reflect year-to-year variations in both food supply and nutrient-energy balance, although the exact relationship is unclear (Chapter 6:I). Consequently, results of analyses using these indices are discussed in terms of both food supply and nutrient-energy balance. Recall that garbage supply within YNP is assumed to have been essentially 0 during 1971-81. So, during those years, values for TFS-NEB are equal to those for NFS-NEB, and values are the same for pre-, post-, and circumnatal periods (Table 4:5).

4:VI. SUMMARY

1) Food supply and nutrient-energy balance for bears (FS-NEB), as for other mammals, apparently tend to be negatively correlated with latitude. At high latitudes, total energetic input from the sun and mean temperature are lower, the growing season for plants is shorter, energetic costs of thermoregulation are higher, and the winter fasting (hibernation) period for bears is longer.

2) According to findings by Rausch (1961), age-specific body weights and rates of growth are positively correlated with food supply

and nutrient-energy balance in black bears, as seems typical among mammals. So the same is probably true for other bears.

3) Limited data substantiates the long-standing observation that body weights of grizzlies tend to be higher in coastal habitats than in inland habitats at comparable latitudes. Apparently nutrient-energy balance is higher on the coasts, due to better food supply and milder climate.

4) Together, latitude and habitat type (coastal vs. inland) statistically account for at least 74% of variance in body weights of ≥4-year-old grizzlies. Younger age-classes show similar relationships.

5) Consequently, where specific data are lacking on food supply or nutrient-energy balance, surrogate indices can be derived from data on body weight (or size), latitude, habitat type, or climate. In Chapter 5 these shall be used to estimate impacts by food supply and nutrient-energy balance on levels and rates of reproduction and recruitment.

6) An index for the supply of edible garbage in Yellowstone National Park was derived from data on number of human visitors each summer. Picton's (1978) climatic index was used as an index of natural food supply and of individual nutrient-energy balance for the bears. Together, the garbage supply and natural food supply and nutrient-energy balance indices constitute an index for total (manmade and natural) food supply, and secondarily for mean nutrient-energy balance of the bears (TFS-NEB). Division of TFS-NEB by population

density (TFS/N-NEB) or biomass (TFS/BM-NEB) should provide increasingly better indices of nutrient-energy balance--and poorer indices for food supply per se. So use of all 3 indices should be reasonably revealing about both food supply and nutrient-energy balance.

CHAPTER 5

RESULTS

Tests are made for positive correlations between parameters of reproduction and recruitment vs. food supply and individual nutrient-energy balance. Comparisons among grizzly populations are presented first. That is followed by comparison among years for grizzlies within Yellowstone National Park.

5:I. COMPARISON AMONG GRIZZLY POPULATIONS

Stringham (1980) and Bunnell & Tait (1981) reviewed evidence for grizzly bears that generation length and interbirth intervals--both inverse indices of maturation rate--were longer and litter sizes were smaller in habitats with poorer food supplies. That reproductive information, along with more recently published data on 2 more populations, was summarized in Table 3:1 (p.26). Below, this is assessed relative to mid-latitude and type (coastal vs. inland) of each habitat.

5:I.A. Maturation Rate, Generation Length, and Interbirth Interval

Data in Table 3:1 indicates that generation length was about 3 years shorter (5.3 vs. 8.2 years, t = 5.1, P:1t=0.001) and interbirth interval a half year shorter (3.2 vs. 3.8 years, T = 1.9, P:1t=0.05) for grizzlies on the coasts of Alaska (n=3) than for those (n=5) occupying inland habitats in Alaska and northern Canada. (Note that faster maturation by grizzlies in the coastal habitats may have also been promoted by the fact that they are at lower latitudes than these particular inland habitats; the coastal vs. inland habitats averaged 58 vs. 67 degrees north, respectively [t = 4.1, P:2t=0.006]). Generation length and interbirth interval for inland habitats farther south in Canada (Glacier National Park) and in the United States (Yellowstone National Park) were comparable to those on the coasts of Alaska.

It is predictable from the negative correlations between body weight vs. latitude for grizzly populations (Tables 4:2 and 4:3, Fig. 4:4), that maturation rates to weaning and to first whelping would be negatively correlated with latitude, due to positive correlations with nutrient-energy balance. That prediction is consistent with the positive correlations between latitude vs. interbirth interval and generation length. Among 7 inland grizzly populations, latitude statistically accounts for 75% (P:1t=0.007) of the variance in interbirth interval (Fig. 5:1)--reflecting primarily variance in age at weaning--and 70% (P:1t=0.01) of that in age at first whelping (generation length) (Table 5:1). As expected, interbirth interval and generation length were shorter--maturation rate was faster--in the coastal habitats than latitude alone would account for relative to inland habitats. Together, latitude and habitat type account for 77% of the variance in interbirth intervals and 80% of that in generation length (P:1t<0.003) for all 10 inland and coastal populations. Note that when all 10 populations are considered, inclusion of both

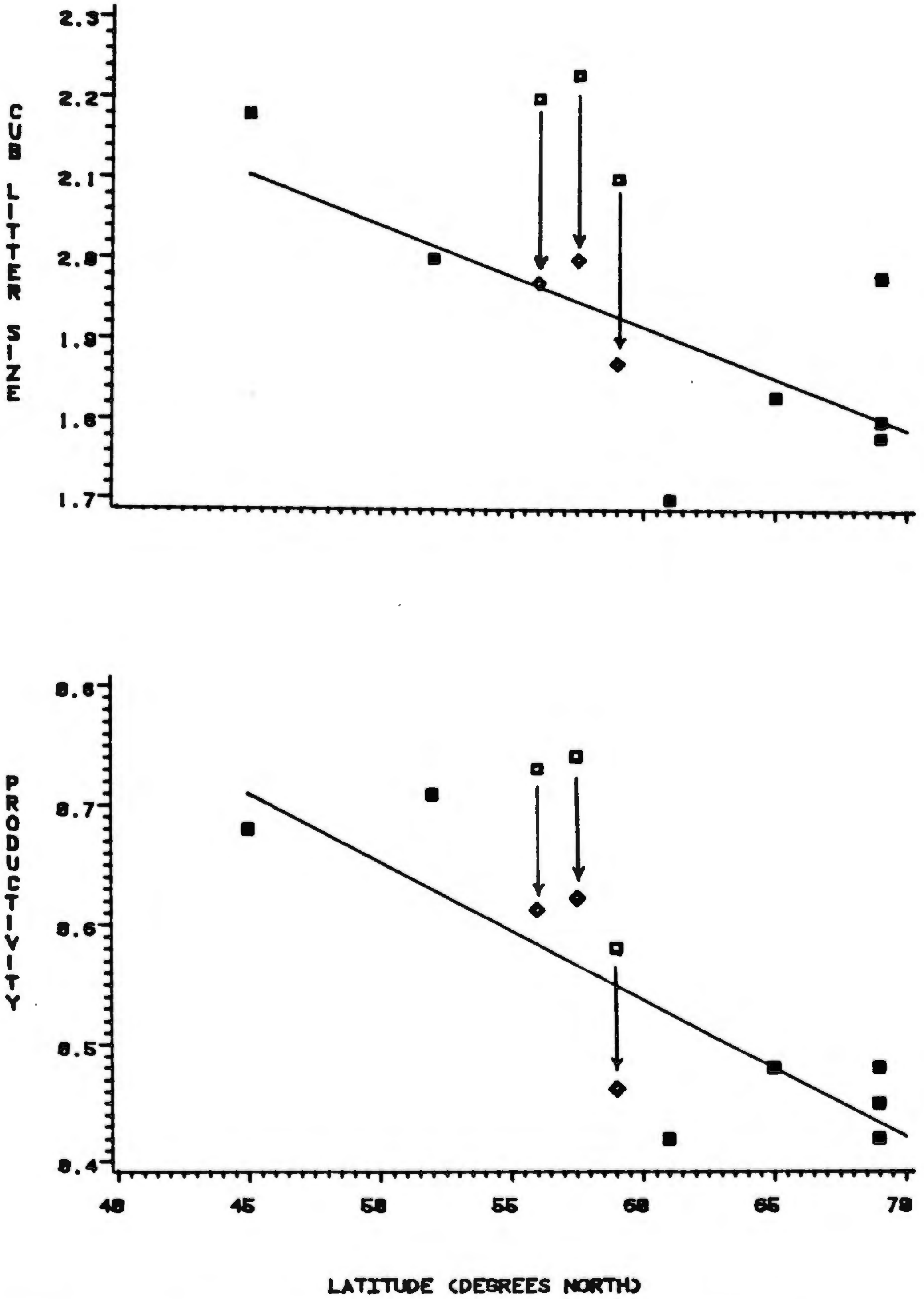


Fig. 5:1. Reproductive parameters regressed on approximate mid-latitude of the habitat for each of 10 North American grizzly populations (◻ inland, ■ coastal). (Data from Table 3:5; see Table 5:1 for r and P:1t).

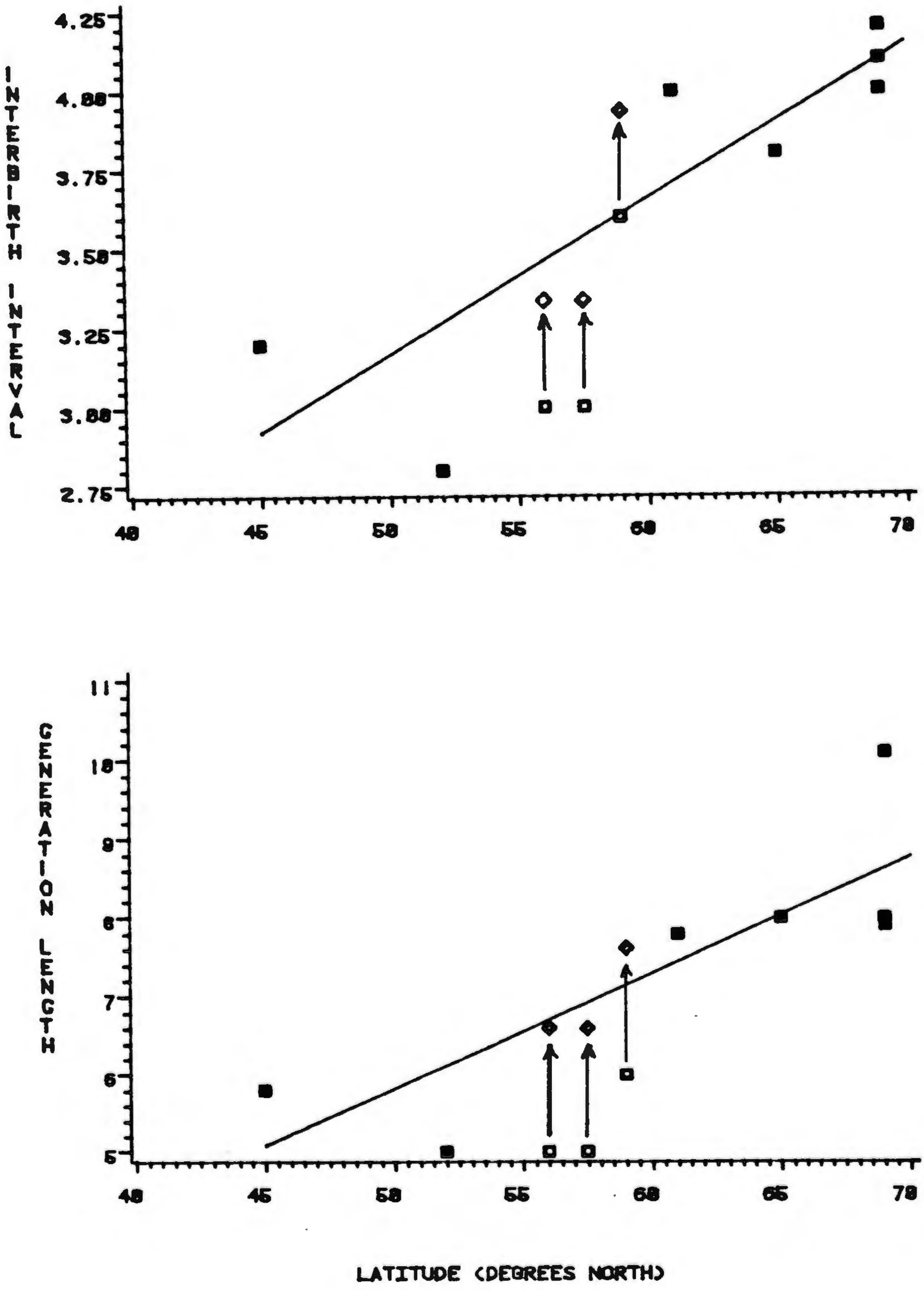


Fig. 5:1. (Continued)

Table 5:1. Parameters of reproduction correlated with habitat type (coastal vs. inland) and latitude (degrees North) for grizzly bear populations.*

Reproductive Parameter	Habitat[1,2] Type (10)	Latitude		Latitude[3] & Habitat Type (10)
		Inland Only (7)	Coastal & Inland (10)	
Interbirth	0.486	0.867	0.824	0.877
interval (IBI)	0.07	0.006	0.002	0.003
Generation	0.606	0.837	0.787	0.897
length (G)	0.03	0.01	0.004	0.002
Litter size	-0.699	-0.717	-0.658	-0.864
(C/L)	0.01	0.03	0.02	0.004
Productivity	-0.588	-0.875	-0.792	-0.893
C/L/IBI	0.04	0.005	0.003	0.002
Reproductive	-0.589	-0.858	-0.791	-0.893
Vigor Index	0.04	0.007	0.003	0.002

* Data from Table 3:1. Values given on the Table are the Pearson correlation r, and probability that reproduction is not best where food supply and nutrient-energy balance are highest (P:1t). Because food supply and nutrient-energy balance tend to be negatively correlated with latitude and habitat type (coastal = 0, inland = 1), all reproductive parameters except generation length and interbirth interval--inverse indices of maturation rate--should be negatively correlated with latitude and habitat type. That includes proportions of cubs and yearlings in the populations.

[1] Sample size (n) is the number of populations sampled, and is given at the head of each column.

[2] Because the coastal populations are at latitudes intermediate between the inland populations in Alaska and northern Canada vs. those in southern Canada and Yellowstone National Park, correlations between parameters of reproduction, recruitment, and infrastructure vs. habitat are probably not much biased by the intervening effects of latitude. However, the relative effects of latitude are best judged through the multiple correlation tests.

[3] Multiple correlation coefficients were deflated by Wherry's (1931) formulated (as cited by Schmitt et al. 1977); see text.

latitude and habitat type in the model yields correlation coefficients only moderately stronger than those obtained above for just inland habitats using latitude as the only independent variable. That is because among these particular 7 inland populations, only those at Glacier and Yellowstone National Parks are at latitudes lower than the 3 coastal populations.

Interbirth interval and generation length were not regressed directly vs. mean adult body weight; for data on both of those parameters and on body weight is not available from enough populations for such tests to yield meaningful results. Nevertheless, correlations between latitude vs. (a) body weight, and vs. (b) interbirth interval and generation length, are strong enough to suggest a significant positive correlation between mean adult body weight vs. rates of maturation to weaning and to first whelping, across these populations. As would be expected from the negative correlation between population density vs. latitude, rates of maturation to weaning and to first whelping are positively correlated with population density (r^2=82% and 80% typ, respectively, P:1t<0.01 Table 5:2; Fig. 5:2).

Those coefficients of determination were calculated without taking into account data on Kodiak Island, since density around Karluk Lake was 10-fold higher than densities in other populations; that is improbably higher than one would expect as an average over the entire annual range of the bears which aggregate at Karluk to feed, primarily

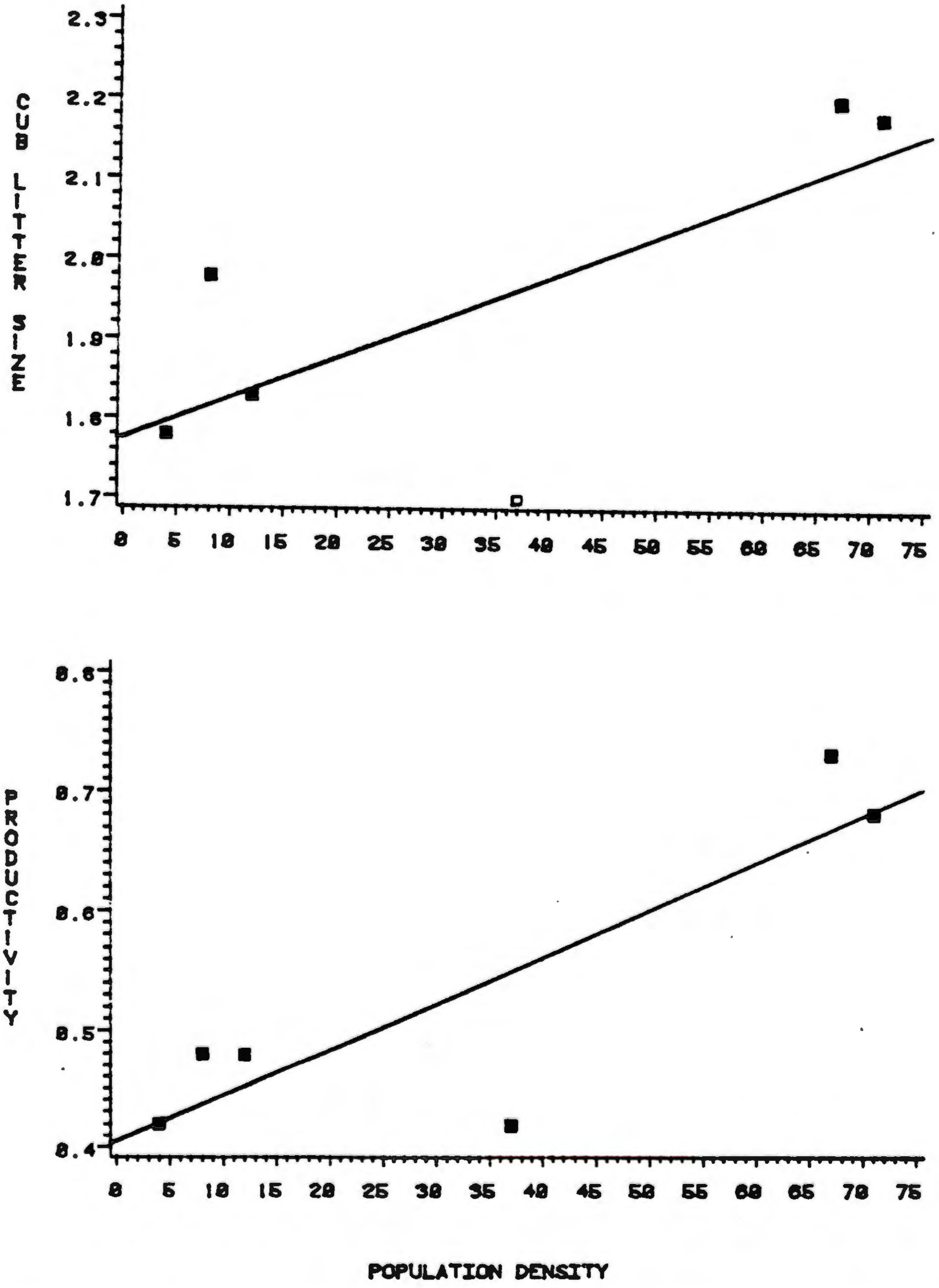
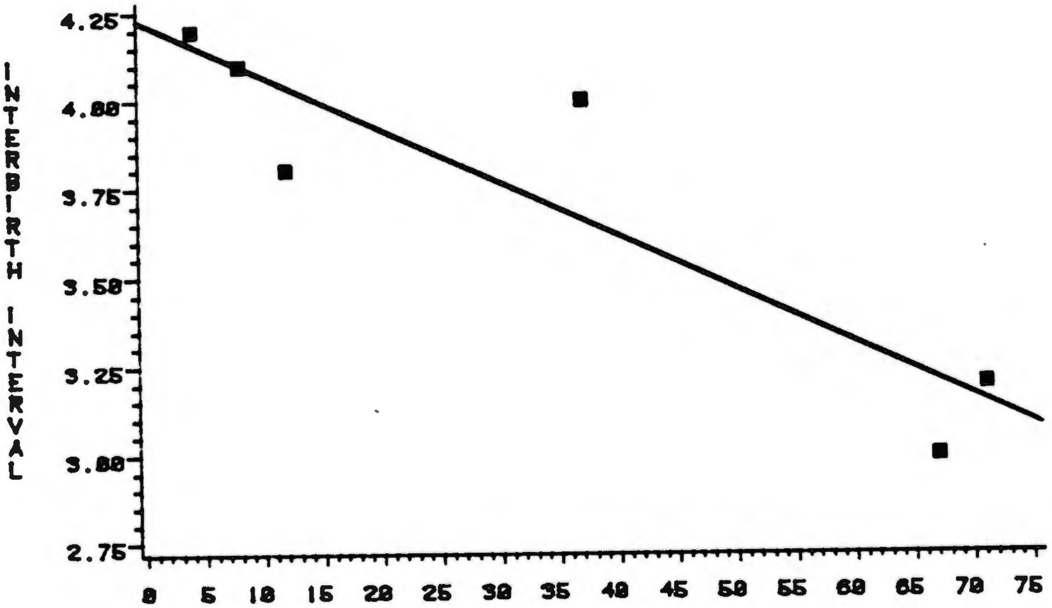


Fig. 5:2. Reproductive parameters regressed on population density in each of 6 North American grizzly populations. (■ inland, □ (Data from Tables 3:1 and 4:1; see Table 5:2 for r and P:1t).



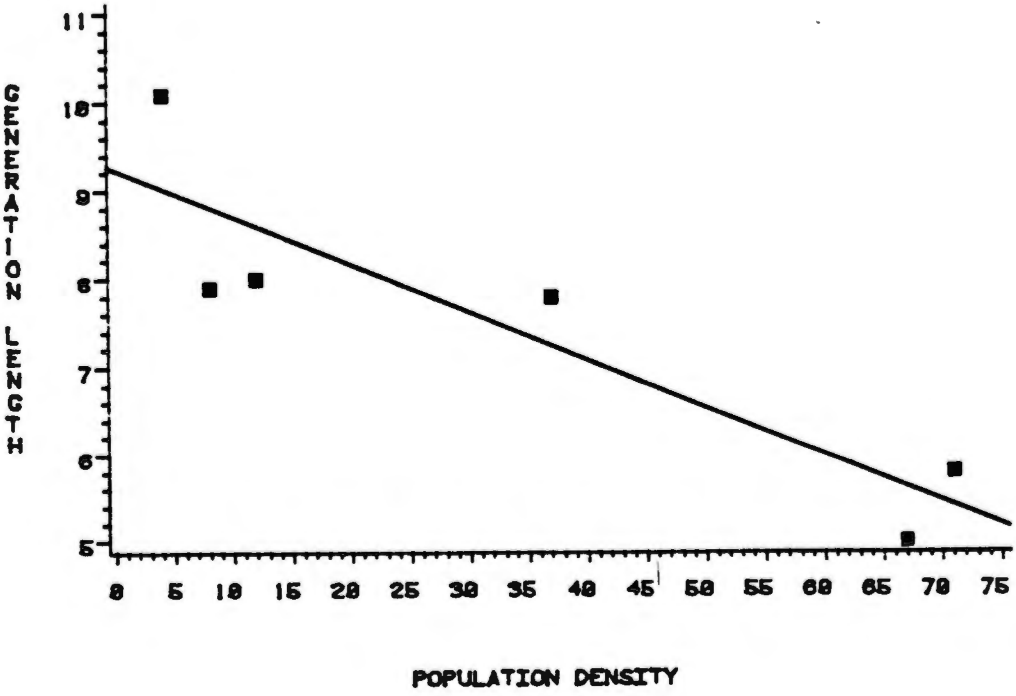


Fig. 5:2. (Continued)

Table 5:2. Parameters of reproduction correlated to population density for 7 grizzly populations.

Reproductive Parameter	Without Kodiak Island	With Kodiak Island
Interbirth interval (IBI)	-0.908 0.006	-0.602 0.08
Generation length (G)	-0.897 0.007	-0.579 0.09
Litter size (C/L)	+0.794 0.05	+0.562 0.09
Productivity (C/L/IBI)	+0.862 0.01	+0.616 0.07
Reproductive Vigor Index (RVI)	+0.870 0.01	+0.604 0.08

* Data from Tables 3:1 and 4:1. Values given are r and P:1t.

on spawning salmon. Results obtained with the Kodiak Island data also included are given in Table 5:2.

5:I.B. Litter Size, Productivity, and Reproductive Vigor

Latitude accounts for 51% (P:1t=0.03) of variance in cub litter size (C/L) among the 7 inland grizzly populations (Table 5:1). Because of relationships between latitude vs. interbirth interval and generation length for the inland populations, latitude also accounts for 76% (P:1t=0.01) of variance in productivity (C/L/IBI) and 74% (P:1t=0.007) of that in reproductive vigor (i.e., in effects of reproductive rate on population growth rate (Fig. 5:1).

For all 10 inland and coastal populations, latitude and habitat type together account for 67%, 74%, and 74% (P:1t$\leq$0.004) of total variance in litter size, productivity, and reproductive vigor, respectively.

Interbirth interval, generation length, productivity, and reproductive vigor--but not litter size--were lower at McNeil River than for the other coastal populations at similar latitudes. Indeed, McNeil values were comparable to what the regressions predict for inland populations at that latitude. Possible explanations are considered in Chapters 6:VII. and 7:III.B.

5:II. COMPARISON AMONG YEARS FOR YELLOWSTONE GRIZZLIES

Yellowstone grizzlies are the only *Ursus arctos* population for which data is available from enough years to support analysis of how population dynamics respond to annual variations in food supply and nutrient-energy balance. This analysis is based on demographic data of J. Craighead et al. (1969, 1974, 1976), F. Craighead (1979), Cole (1974), and Knight et al. (1977, 1981, 1982). Due to lack of direct data for supplies of natural and manmade foods, these values are estimated from indices of natural food supply and nutrient-energy balance (climate) and of garbage supply, as noted in Chapter 4.

5:II.A. Impacts of Closing the Garbage Dumps

After 1968, when garbage supply in YNP began to decline, reproductive level also declined. Mean annual litter size fell 16.5% from 2.24 during 1959-68 to 1.87 during 1972-81, after closure of dumps had been completed. Density of cub litters per cohort (whelping level) dropped 18.4%, and density of cubs per cohort dropped 30.8%. Those changes, as well as ones relative to other post-closure periods, are shown in Table 5:3.

The extent to which the decline in reproductive level associated with closure was due to closure per se is a matter of continuing debate. Members of the Craighead research team (e.g., J. Craighead et al. 1974; F. Craighead 1979) attributed the reproductive decline to (1) changes in the amount of garbage available as food to the grizzlies, and (2) to removal of numerous bears from the population--mainly bears which had responded to dump closure by seeking alternative sources of manmade food or which had otherwise endangered people or property. By contrast, Picton (1978) attributed

Table 5:3. Changes in reproductive level and climate associated with closure of the Yellowstone garbage dumps during 1968-71: before (1959-68) vs. after (1972-81) comparison.*

Years	#Cubs[1]	#Cub[2] Litters	Mean Annual Cub Litter Size	Climate Index
1959-68	32.8	14.7	2.24	+1.6
1972-81[3]	22.7	12.0	1.87	-2.5
Change	-30.8%	-18.4%	-16.5%	-4.1%
P:1t	0.003	0.05	0.0005	0.03
1959-68	32.8	14.7	2.24	+1.6
1969-81	23.6	12.5	1.87	-1.9
Change	-28.0%	-15.2%	-16.5%	-3.5
P:1t	0.002	0.05	0.0001	0.02

* Values given are for the unweighted means for cohorts *conceived* before vs. after dump closure *began*, percentage change in reproductive level, and 1-tailed significance level from t-test for declines in reproductive level.

[1] Cub density.

[2] Whelping level.

[3] The year 1972 was chosen here, rather than 1971, for start of the post-closure period because production of cubs in 1981 might have been influenced by food supply in 1970, i.e., prenatally, while a substantial amount of garbage might still have been available within YNP. The effects of garbage supply during the period of dump closure are best revealed by the contrast between changes from 1959-68 vs. 1972-81 against 1959-68 vs. 1969-81.

the decline in reproduction largely to coincidental worsening of the climate.

A key to resolving that controversy lies in (a) comparing the relationships between litter size vs. climate before vs. after start of dump closure, via multiple regression and analysis of covariance.

1959-81: $C/L = 2.19 + 0.0294*CI - 0.260*DC + 0.000250*(CI*DC)$ ($R = 0.843$, $P:1t < 0.0001$ overall; $P:1t=0.006$ for CI, 0.001 for DC; $P:2t > 0.99$ for CI*DC). Again, the slope of the equation, the CI term, represents the amount of change in litter size per unit change in climate, independently of any simultaneous decline induced by dump closure. The relationship between litter size vs. climate is represented by 2 parallel lines in Fig. 4:7 (p.80), the upper line for the pre-closure period (1959-68), the lower for the post-closure period (1972-81). The litter size decline induced by dump closure (DC) independently of climatic change, is approximated by the DC term (0.260 C/L) of the multiple regression equation, and appears in Fig. 4:7 as the vertical separation between the before vs. after lines. The specific impact of dump closure is dramatically illustrated by the rapid change in sizes of litters born during 1968-70, as marked by the steepest regression line in Fig. 4:7 (p.80).

The 1959-68 vs. 1972-81 cohorts were born following winters when the climate index averaged +1.6 vs. -2.3, a drop of 3.9 units. According to the slope of the multiple regression equation, that could account for a decline in mean annual cub litter size of only 0.115 C/L ($=0.0294*3.9$), or about 31% of the observed 0.37 C/L decline in litter size from 2.24 to 1.87. That equation also attributes 0.26 C/L or 70% of that 0.37 C/L decline to dump closure per se. Thus, climatic worsening and dump closure together account for essentially all of the difference in mean litter sizes before dump closure began vs. after it was completed, with the impact of closure having been more than twice as great as that of climate. (The fact that the apparent contributions by climate and dump closure sum to 101% rather than to 100%, is just a sampling artifact of negligible importance for the purposes of this analysis).

Although the presence of abundant garbage would have buffered effects of climatic fluctuation on litter size, dump closure did not alter either slope of the regression line or magnitude of the correlation (before: $r = 0.666$; after: $r = 0.657$; P:1t < 0.02). The fact that the regression lines for the periods before vs. after dump closure began are parallel indicates that amount of change in litter size per unit change in climate was not affected by loss of garbage as a food source or by other effects of dump closure. This is consistent with the fact that both regression lines are linear. In other words, amount of change in litter size per unit change in climate was the same at all observed levels of climate, and presumably of natural food supply and nutrient-energy balance. So, if garbage supply were put into units equivalent to those for climate (see Chapter 4:III.E.), a change in the amount of garbage would be equivalent to a change in climate index, and would follow the <u>same</u> linear slope.

Even though the -3.9 unit change in climatic means between 1959-68 vs. 1972-81 seems to have had less than half as much impact as dump closure on mean litter sizes, that does not indicate that climatic variation typically had less impact than variation in supply of manmade foods at YNP. For example, the -20 unit change in climate from the most favorable observed conditions (+8 in 1963) to the most severe (-12 in 1975) would have tended to cause a drop in litter size of about 0.6 C/L (= 20*0.029), independently of the approximately 0.3 C/L decline due to dump closure. Even greater climatic changes would have tended to have had even stronger impacts on reproductive rate.

5:II.B. Reproduction and Recruitment vs. Food Supply and Nutrient-Energy Balance

When data are considered over the full 23 years from 1959-81, discussion of correlations between reproductive parameters vs. food supply and nutrient-energy balance is restricted to the index for total food supply and nutrient-energy balance (TFS-NEB), since that is the only one which could be estimated for that whole period. Lack of data on population density (N) and biomass (BM) past 1970 prevents one from calculating supply per bear (TFS/N-NEB) or per unit bear-mass (TFS/BM-NEB) past 1970. However, during 1959-70, when all 3 indices could be calculated, all were similarly correlated with all parameters of reproduction and recruitment--although supply per bear tended to be a slightly better (P:1t=0.01) predictor than total supply, and supply per unit bear mass tended to be better still (P:1t<0.0001). This is probably related to TFS-NEB being the best index of these for total food supply, whereas TFS/N-NEB and TFS/BM-NEB should be increasingly better indices for average individual nutrient-energy balance. The meaning of differences between results obtained with each of the 3 indices shall be discussed in Chapter 6:X. In any event, in order to simplify presentation, values given in Tables 5:4 and 5:5 are averaged across all 3 indices--as indicated by the less specific phrase "food supply and nutrient-energy balance" (FS-NEB).

$$\left.\begin{array}{l}\text{TFS-NEB}\\ \text{TFS/N-NEB}\\ \text{TFS/BM-NEB}\end{array}\right\}\ \text{FS-NEB}$$

Data on mean annual cub litter size, litter density (whelping level), and cub density for Yellowstone grizzlies is available from the 23-year period 1959-81. The other parameters of reproduction and recruitment were documented only during the 12-year period 1959-70. The indices for food supply and nutrient-energy balance (FS-NEB) can be calculated for all of the years during 1959-70 except 1969. Thus, none of these parameters of reproduction and recruitment could be evaluated relative to postnatal level of food supply and nutrient-energy balance for the 1969 cohort or relative to the prenatal level of FS-NEB for the 1970 cohort. That has important consequences for interpreting the results presented here.

Levels of reproduction and of food supply and nutrient-energy balance during 1970 were especially low, compared to levels during 1959-68, apparently due largely to the impacts of dump closure.

Table 5:4. Reproductive parameters correlated to indices for food supply and nutrient-energy balance for Yellowstone grizzlies.*

	Period When FS-NEB Was Measured		
Parameter	Prenatal	Postnatal	Circumnatal
<u>1959-81</u> [1]			
Cub litter size [2]	0.823	0.855	0.863
(C/L)	0.0001	0.0001	0.0001
Whelping level	0.526	0.536	0.533
(#L)	0.006	0.005	0.006
Cub density	0.697	0.705	0.713
(#C)	0.0002	0.0001	0.0002
<u>1959-70</u> [3]			
Cub litter size	0.673	0.819	0.825
(C/L)	0.01	0.001	0.005
Whelping level	-0.363	0.172	-0.341
(#L)	0.85	0.31	0.82
Whelping rate	-0.208	0.242	-0.167
(#L/AdF)	0.71	0.24	0.67
Interbirth interval [4]	0.628	0.716	0.624
(IBI) (P:2t)	0.047	0.01	0.055
Cub sex ratio [5]	-0.113	0.221	0.090
(%MC)	0.64	0.25	0.67
Male cub density [6]	-0.083	0.346	-0.042
(#MC)	0.58	0.15	0.55
Female cub densty [6]	0.24	0.108	0.029
(#FC)	0.48	0.37	0.46
Total cub density	-0.093	0.498	-0.037
(#C)	0.61	0.06	0.54

Table 5:4. (Continued)

[*] Values given are the Pearson correlation coefficient (r) and probability $r \ngtr 0$ (P:1t).

[1] For 1959-81, sample sizes are 22 years pre- and postnatally, but 21 years circumnatally for all 3 reproductive parameters. Only the index for total food supply and nutrient-energy balance is represented here since data on population dynamics and biomass were not available after 1970.

[2] Regressions of cub litter size vs. indices of food supply and nutrient-energy balance are linear (A-A); but all of the other relationships are semi-logarithmic (A-L) (see text).

[3] For 1959-70, sample sizes are 10 years prenatally, 11 postnatally, and 9 circumnatally, for all reproductive parameters. Values given are means averaged across all 3 indices for food supply and nutrient-energy balance: TFS-NEB, TFS/N-NEB, and TFS/BM-NEB.

[4] No a priori prediction could be made as to whether interbirth interval would be positively or negatively correlated with food supply and nutrient-energy balance; for it could not be predicted whether the "positive" effects of FS-NEB on recruitment rate would dominate the "negative" effects on maturation rate, or vice verse (see text and Fig. 6:1). So a 2-tailed test of significance was used. For all other parameters, 1-tailed tests were used for predicted positive correlations.

[5] Values for cub sex ratio during 1965, 1966, and 1969, were estimated from the regression of cub sex ratio on cub density (Chapter 3:I.D.2).

[6] Densities of male and female cubs each year were estimated by multiplying sex ratio for sampled cubs against total cub density (Chapter 3:I.D.2).

Table 5:5. Recruitment parameters correlated to indices for total food supply and nutrient-energy balance, supply per bear, and supply per unit bear-mass.

Parameter 1959-70	Total Food Supply & Nutrient-Energy Balance Prenatal (t-1)	Postnatal (t)	Circumnatal (t-1 & t)
Cohort size at age			
0.5 yr in yr t	-0.093 0.60 (10)	0.498 0.06 (11)	-0.037 0.53 (9)
1.5 yrs in yr t+1	0.337 0.17 (10)	0.352 0.16 (10)	0.381 0.15 (9)
2.5 yrs in yr t+2	0.478 0.09 (9)	0.503 0.07 (10)	0.495 0.09 (9)
5.5 yrs in yr t+5	0.836 0.01 (6)	0.768 0.02 (7)	0.803 0.02 (6)
Recruitment rate between ages			
0.5 - 1.5 yrs yrs t - t+1	0.498 0.06 (10)	0.487 0.08 (10)	0.520 0.07 (9)
0.5 - 2.5 yrs yrs t - t+2	0.600 0.04 (9)	0.617 0.03 (10)	0.611 0.04 (9)
0.5 - 5.5 yrs yrs t - t+5	0.741 0.06 (6)	0.672 0.05 (6)	0.708 0.06 (6)

* Correlation values (r, P:1t, n) given were averaged across all 3 of those indices. Hypothesis tested $r \not> 0$. All models are semi-logarithmic.

Consequently, the lack of a FS-NEB datum for 1969 tends to obscure the prenatal effects of dump closure on reproductive parameters documented only during 1959-70, whereas the presence of a FS-NEB datum for 1970 reveals the initial postnatal effects of dump closure. For that reason, the reproductive parameters tend to be more positively correlated with each index for food supply and nutrient-energy balance postnatally than prenatally. In other words, that difference seems to be a sampling artifact, not an indication that reproduction (assessed at age 0.5 year) and recruitment were affected by food supply and nutrient-energy balance more postnatally than prenatally.

For Yellowstone grizzlies, there is no evidence of a positive correlation for food supplies between consecutive years ($r = 0.046$ prior to dump closure and -0.641 after closure began). So a positive correlation between a parameter of reproduction or recruitment vs. postnatal food supply and nutrient-energy balance is not likely to be a spurious consequence of a positive correlation vs. prenatal food supply and nutrient-energy balance, or vice versa.

5:II.B.1. Litter Size

Litter size was directly linearly proportional to the indices for food supply and nutrient-energy balance (Fig. 5:3a). In other words, change in litter size per unit change in the level of total food supply and nutrient-energy balance (TFS-NEB) was apparently the same at all observed levels--although that need not be true at yet lower or higher levels of TFS-NEB. (1) Mean litter size cannot

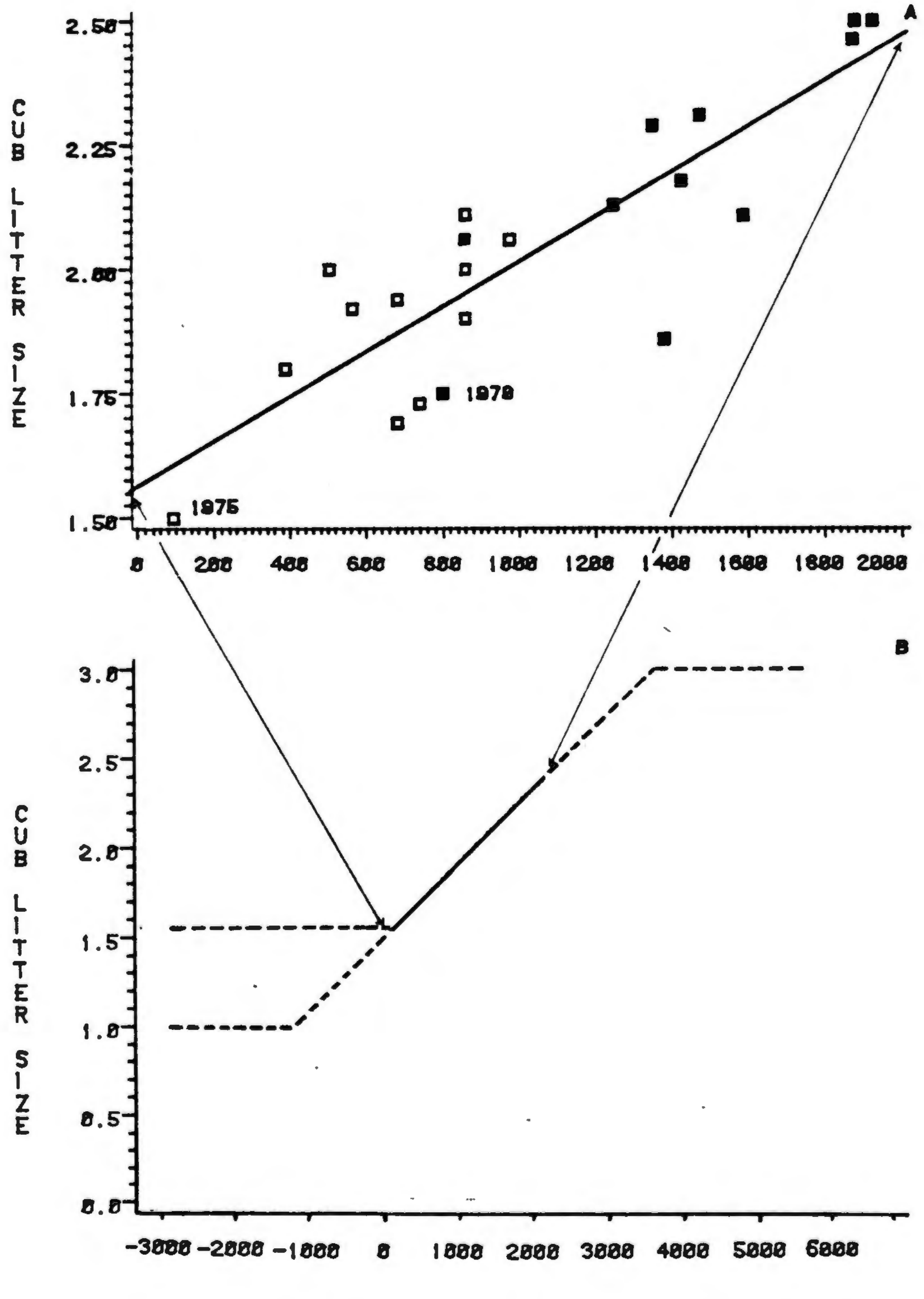


Fig. 5:3. Cub litter size regressed on the index for total food supply and nutrient-energy balance postnatally, for Yellowstone grizzlies. (a) Regression plot fit to data (o 1959-70, o 1971-81). (b) Extrapolation of that plot up to the expected maximum of 3.0 C/L and down the minimum of 1.55 C/L at 0 TFS-NEB, below which reproduction does not occur, and down to the theoretical absolute minimum of 1.0 C/L (see text).

decline below 1 C/L. Data on whelping rate suggests that most females may cease whelping while food supply or their own nutrient-energy balance are still high enough for production of a single cub--perhaps because they would not be able to successfully rear even a single cub under those conditions. (2) There also has to be some upper limit to litter size. When food supply and nutrient-energy balance far exceed the average bear's needs--at levels higher than what occurred in YNP during 1959-81--the litter size plot should eventually plateau (Fig. 5:3b), probably near 3.0 C/L (Chapter 8:II.B). Larger cub litters seem rare in this and other grizzly populations (Stringham, in prep). Even in Pennsylvania, where prime adult female black bears often produce litters of at least 4 cubs (Alt 1982), this may represent a genetically determined higher per capita reproductive rate selected by long term high food supply and nutrient-energy balance, rather than being a facultative response.

5:II.B.2. Whelping Level and Rate

Whelping level, the annual density of cub litters produced and surviving to age 0.5 year, was positively correlated with food supply and nutrient-energy balance. As food supply and nutrient-energy balance rose or fell, whelping level rose or fell proportionately.[1]

---

[1] "Rise" and "fall refer here only to movement of the reader's attention relative to the axes of the plot, not to changes in food supply or whelping level over time. That restriction applies to all figures within this dissertation where change over time is not specifically designated, for instance by a derivative with respect to time [e.g., dFS/dt]).

By contrast, sensitivity to change in the level of food supply and nutrient-energy balance (TFS-NEB) was inversely related to the average level of TFS-NEB. When food supply and nutrient-energy balance were low, litter density was highly sensitive; but as food supply and nutrient-energy balance increased, litter density became progressively less sensitive. That relationship can be approximated with a semi-logarithmic curve (Fig. 5:4).

By semi-logarithmic it is meant that the relationship is linearized when the parameter of reproduction or recruitment is on an arithmetic scale (A), whereas that for the index of food supply and nutrient-energy balance is transformed to a "natural" logarithmic scale (L). This is indicated in the Tables by the symbol A-L. When both variables are on arithmetic scales the symbol A-A is used; when both are on log scales, L-L is used.

A semi-logarithmic model could be fit to the relationship between whelping level (or any other parameter) vs. TFS-NEB only after all values of TFS-NEB had been made positive; for non-positive numbers do not have logarithms. For 1959-70, the lowest value was 0, which occurred in 1970. So only "1" had to be added to make all values positive for those years. By contrast, the lowest value of TFS-NEB which occurred during 1971-81 was -707, in 1975. Hence, a positive value at least that large had to be added to each TFS-NEB value on the original scale. The value arbitrarily chosen was 800. To facilitate comparison among parameters, all are graphed on the +800 scale.

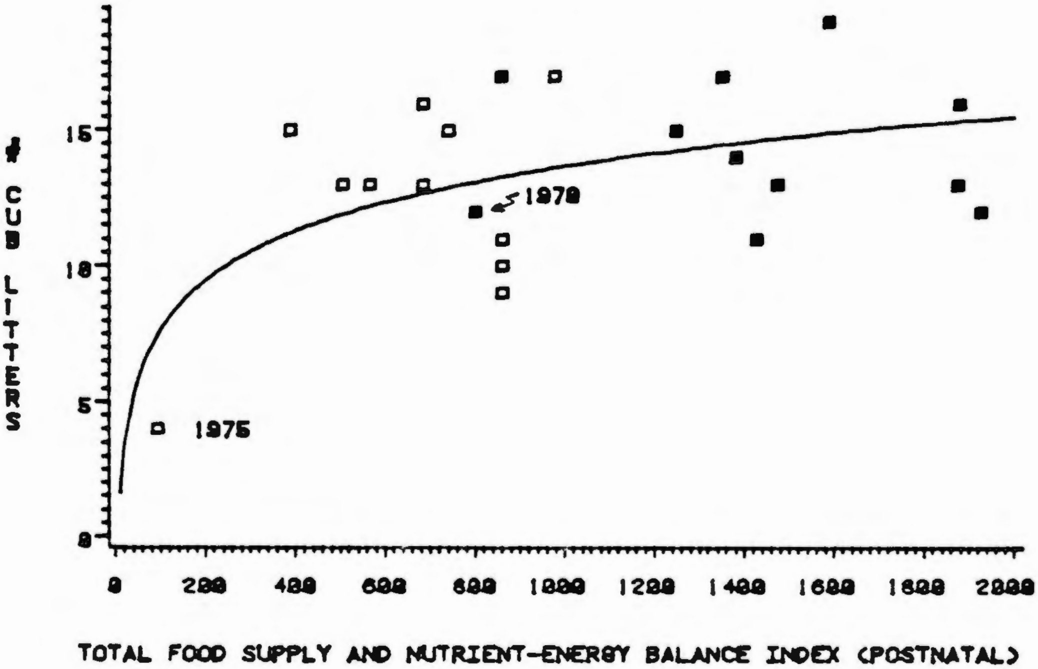


Fig. 5:4. Whelping level regressed on the index for total food supply and nutrient-energy balance postnatally, for Yellowstone grizzlies (■ 1959-70, ◻ 1971-81).

Even after addition of 800, "0" TFS-NEB still does <u>not</u> represent a total lack of food or energy. Rather, it approximates the level below which no cubs reached age 0.5 year, if any were born at all--the threshold below which nearly all food consumed by a female was utilized for her own maintenance and growth. That threshold was closely approached in 1975 when only 4 females were found with cubs and litter sizes averaged 1.5. Additional research will be needed to establish how much food is actually represented by each unit of the TFS-NEB index and to determine the actual minimum thresholds of food supply and nurient-energy balance necessary for successful reproduction by grizzlies.

Let it be emphasized that even the semi-logarithmic relationship between whelping level vs. food supply and nutrient-energy balance is evident only when one has data ranging from fairly low to fairly high levels of food supply and nutrient-energy balance. When one has data only for periods when the levels were usually high, as during 1959-68, whelping level appears uncorrelated with FS-NEB. Only after dump closure did food supply and nutrient-energy balance fall so low as to induce and reveal the correlation and semi-logarithmic relationship. When only data for 1959-70 is considered (Fig. 5:4), it is only the 1970 datum for food supply and nutrient-energy balance that was low enough to induce a weak positive correlation with concurrent whelping level. The fact that no such correlations are apparent between whelping level vs. pre- and circumnatal FS-NEB stems from the lack of a reliable estimate for

FS-NEB during 1969, which is prenatal to litters born in 1970. Again, this point is crucial for interpreting findings on whelping rate and other parameters for which data are available only from 1959-70.

When whelping level (density of cub litters) is divided by total density of adult females in the population, a figure is obtained for whelping rate (#L/AdF). As food supply and nutrient-energy balance increase, they cannot elevate whelping rate past 100% of the females that were "fertile" during the previous breeding season. Recall that a "fertile" female is one which would be expected to whelp during the given year since she was mature but not lactating during the previous breeding season and should have mated then (see Eiler 1981). Although there was considerable variation from year to year in the proportion of adult females that were fertile, whelping rate should have averaged out to approximately the inverse of the interbirth interval (see Chapter 3:I.B.2). Hence, the curve for whelping rate should eventually plateau near the inverse of the interbirth interval attained at the level of FS-NEB where interbirth intervals are minimized. During 1959-70, annual means for interbirth interval averaged 3.12 years. Despite the fact these intervals are on only 36% of the litters, the inverse of 3.12, 32.1%, closely approximated the average whelping rate of 32.8% (range 23% to 44%) concurrently.

During those years, slopes for regressions of whelping rate and level vs. FS-NEB indices were close to "0." Indeed, those between whelping rate vs. prenatal FS-NEB were non-significantly negative. It is only after dump closure. when the decline in garbage supply and increased climatic severity substantially lowered food supply and nutrient-energy balance, that the full impacts by these factors on whelping level and rate *could* have been detected. Available data on whelping *level* during 1971-81 (Fig. 5:4) enables one to document its response to those low levels of TFS-NEB. But lack of data on density of adult females past 1970 prevents one from doing the same for whelping *rate.* For now, existence of an asymptotic relationship between whelping rate vs. food supply and nutrient-energy balance for Yellowstone grizzlies can only be inferred from (1) basic theory, as explained above, and from (2) data on the correlation between whelping level vs. rate (see below), and (3) data on other mammals, including black bears (Eiler 1981), and reindeer (*Rangifer tarandus*, Reimers 1983), as shall be detailed later.

This inferrence that sensitivity of whelping rate, somewhat like that of whelping level, would have tended to increase as TFS-NEB declined, is supported by the high autocorrelation between whelping rate vs. whelping level

#L vs. #L/AdF

during the years when data was obtained on both parameters. During 1959-70, the correlation was 0.964 ($P:2t<0.0001$). That was due largely to the stability in density of adult females at least during 1964-70 and apparently during 1959-63. (Recall that density of adult females during 1959-63 could only be estimated). Thus, most variation in whelping rate during 1959-70 was due to variation in whelping level. If that stability in adult female density continued after 1970 (despite removal of some of them by humans; see Tables 3:3 (p.31) and 3:6 (p.34), and Chapter 6:IX), then whelping level and rate would have continued to fluctuate together. But even if they did not fluctuate together, so long as density of adult females did not decline _faster_ than whelping level, particularly during 1975, then the relationship between whelping rate vs. TFS-NEB would have been similar to that for whelping level vs. TFS-NEB. Note that for Minnesota black bears too, whelping level was highly autocorrelated with whelping rate ($r = 0.923$, P:2t=0.01), due again largely to stability in density of adult females (data in Table 3:5, p.33).

The asymptotic relationship between whelping rate vs. food supply is even more clearly revealed in Eiler's (1981: Table 17) data for black bears in the Great Smoky Mountains at the border of Tennessee and North Carolina, with the exception of 1 outlying datum (Fig. 5:5; $r^2 = 88.4\%$ typ, P:1t<0.01). The X-intercept of this curve, at the origin, approximates the supply of hard mast (primarily acorns) at which reproduction would completely cease. No positive X-intercept yielded as high a coefficient of determination as did "0" itself; and no negative value yielded a significantly (>4%) better fit; so the curve with the "0" mast supply as its X-intercept is shown in Fig. 5:5. The anomalous datum may represent a year when foods other than hard mast were exceptionally scarce. Or, the index by which mast abundance was indirectly estimated may be perturbated under some conditions. In any event, even when the anomalous datum is taken into

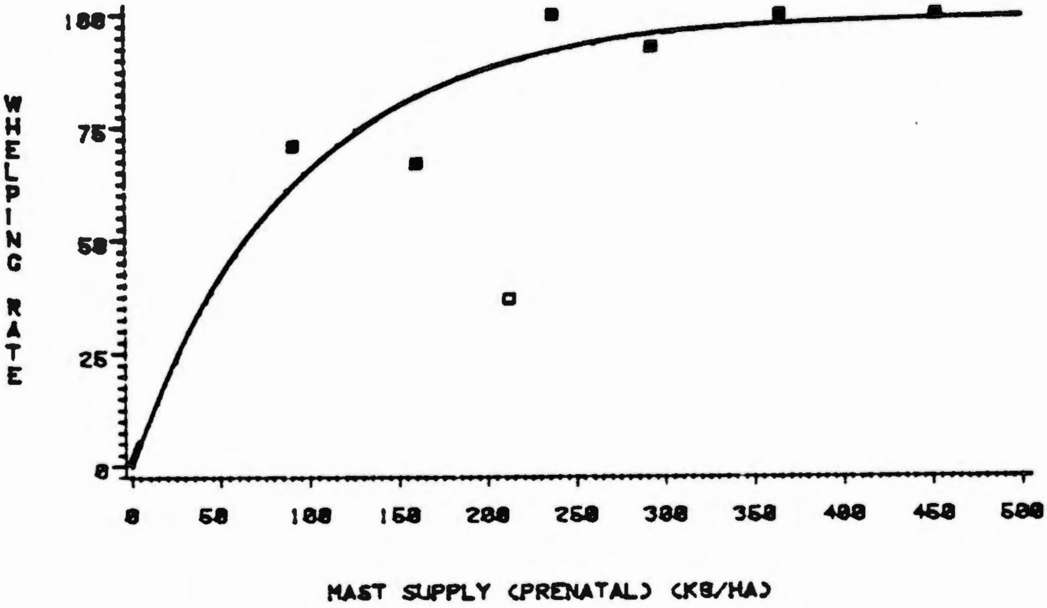


Fig. 5:5. Whelping rate regressed on mast (acorn) supply prenatally for Great Smoky Mountains black bears. (Data from Eiler 1981). The open symbol "□" is an anomalous datum not taken into account when the regression plot was derived (see text).

account, whelping rate averaged 97% (37/38) if hard mast supply prenatally was at least 220 Kg/ha (mean = 336 Kg/ha, n=4 years), but only 61% (17/28 females) if it was less than 220 Kg/ha (mean 154 Kg/ha, n=3 years).

Suppose then that whelping rate in an hypothetical population is asymptotically related to FS-NEB--even if FS-NEB never happens to become high enough for the curve to completely plateau. Then, if density of adult females is completely uncorrelated with FS-NEB, whelping level would also tend to be asymptotically related to FS-NEB. By contrast. if adult female density is negatively correlated with FS-NEB, then the slopes of tangents to the curve for whelping level would be less positive than tangents to the curve for whelping rate. Thus, the weak negative correlation between density of adult females vs. FS-NEB (r = -0.402, P:2t=0.22) explains why the correlations between whelping level vs. FS-NEB indices were less positive than those for whelping rate during 1959-70.

Recapitulating for Yellowstone grizzlies: (1) When food supply and nutrient-energy balance were low, (a) mean litter size for females which succeeded in whelping and in rearing litters to at least age 0.5 year, was affected much less than (b) the number and proportion of adult females that succeeded. (2) By contrast, even when food supply and nutrient-energy balance were so high that most females succeeded in whelping and rearing at least 1 cub to age 0.5 year, litter size was still affected by variations in food supply and nutrient-energy balance. (3) Those characteristics arise from differences in sensitivities by litter size vs. whelping level and rate to low vs. high levels of food supply and nutrient-energy balance. Sensitivity of litter size to FS-NEB was the same at all observed levels of FS-NEB. By contrast, sensitivities of whelping level and probably whelping rate to FS-NEB were inversely related to the average level of FS-NEB, as also seems to have been true for Smoky Mountains black bears.

The relationships between these parameters vs. food supply and nutrient-energy balance are (a) linear for litter size, (b) approximately semi-logarithmic for whelping level, and (c) probably aysmptotic for whelping rate. More data at high and low levels of food supply and nutrient-energy balance will be needed to confirm whether or not these are the best kinds of models for each parameter. For instance, sigmoid models which rise more gradually from the abcissa might be more realistic for some of them, perhaps including cub litter size (see Fig. 4:1).

5:II.B.3. Interbirth Interval

Interbirth interval was positively correlated with food supply and nutrient-energy balance during both the pre- and postnatal periods, and thus circumnatally (Fig. 5:6). One obvious hypothesis is that the positive correlations might arise from effects of food supply and nutrient-energy balance on recruitment to weaning for litters, since dams which lose entire litters tend to have truncated interbirth intervals--so long as the interval between loss of the litter and next

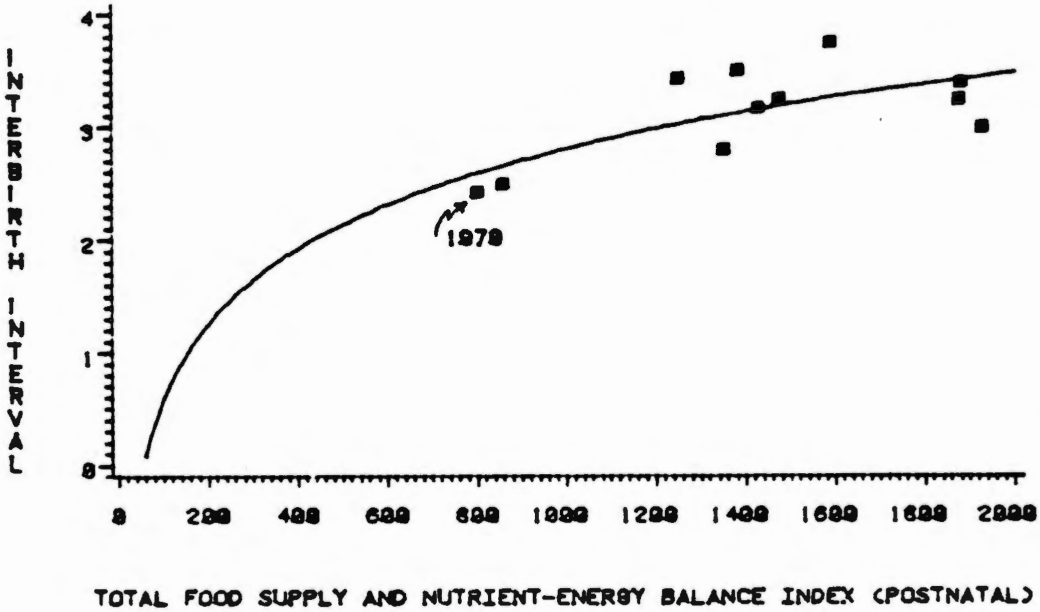


Fig. 5:6. Interbirth interval regressed on the index for total food supply and nutrient-energy balance postnatally, for Yellowstone grizzlies (1959-70).

whelping is not compensatorily increased by low food supply and nutrient-energy balance or by some other factor (see Chapter 6:III.D). However, interbirth interval was only marginally correlated with recruitment rate from age 0.5 to 1.5 years (r = 0.460, P:1t=0.08, n=11), and even more weakly (r = 0.291, P:1t=0.21, n=10) with recruitment rate to age 2.5, when at least half of the litters had been weaned, most or all of the others being weaned by age 3.5. This low correlation is probably an artifact of knowing interbirth intervals for an average of only 36% of the litters censused each year--an hypothesis which could be tested if recruitment rates were known for the same litters as interbirth intervals.

Because food supply and nutrient-energy balance in year t affect interbirth interval, they should affect whelping level and rate in years t+2 to t+4. However, no such correlation is discernible in this data, perhaps because so many other factors, including FS-NEB in years t+1 to t+4, also affect whelping level and rate in years t+2 to t+4.

5:II.B.4. Compound Factor for Reproductive Level

To further elucidate the net impact of food supply and nutrient-energy balance on reproductive level and rate, the 3 aforementioned reproductive parameters--litter size, whelping level, and interbirth interval--were combined into a single Factor via the Principle Component (Axis) method. This Factor was even more highly correlated with food supply and nutrient-energy balance than was any of the individual parameters (r = 0.842, P:1t=0.0006).

5:II.B.5. <u>Cub Density</u>

Recall that during 1959-81, (a) litter size at age 0.5 year was an approximately linear function of postnatal TFS-NEB, and that (b) density of 0.5-year-old litters (i.e., whelping level for the dams) was an approximately semi-logarithmic function. Consequently, their mathematical product

$$C/L * \#L \quad = \quad \#C$$

density of 0.5-year-old cubs in each cohort, can also be closely approximated with a semi-logarithmic function (for postnatal TFS-NEB: r = 0.711, P:1t=0.0001; Fig. 5:7).

Despite the clear positive correlation between cub density vs. food supply and nutrient-energy balance pre-, post-, and circumnatally, during the 23-year period 1959-81, this is obscured when one considers only the half-shorter period 1959-70. Cub density appears only weakly positively correlated with postnatal FS-NEB during just 1959-70, and uncorrelated with prenatal and circumnatal FS-NEB during that period. That is for reasons discussed earlier. Specifically, the presence of a FS-NEB datum for 1970 (postnatal for the 1970 cohort), but absence of a datum for 1969 (prenatal for the 1970 cohort), reveals the initial postnatal but not prenatal impacts of dump closure. Furthermore, relative weakness of the correlation between cub density vs. postnatal food supply and nutrient-energy

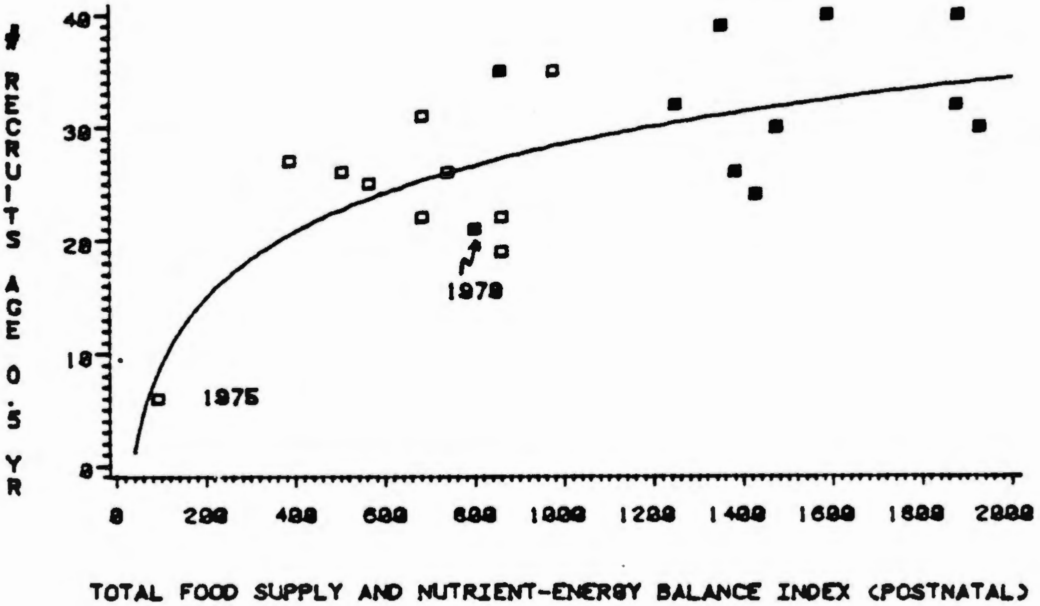


Fig. 5:7. Cub (0.5 yr) cohort size regressed on the index for total food supply and nutrient-energy balance postnatally, for Yellowstone grizzlies (■ 1959-70, □ 1971-81).

balance manifests only the lack of response by these reproductive parameters to variations in the level of food supply or nutrient-energy balance when that level was high (1959-68), not lack of response overall (1959-81). That point has been stressed again since it is also crucial for interpreting the data on cub sex ratio and on recruitment to ages 1.5-5.5, which is available only from 1959-70, as shall be shown below.

5:II.B.6. Cub Sex Ratio

Again, it is the presence of a datum for food supply and nutrient-energy balance from 1970 but not from 1969 which accounts for a positive correlation between densities of cub litters and of cubs postnatally but not pre- and circumnatally, when one considers data only from 1959-70--although there are clear positive correlations at all 3 time-lags when data are considered from the entire 23-year period 1959-81. So those factors might also account for cub sex ratio also being positively correlated with food supply and nutrient-energy balance postnatally, but not pre- and circumnatally (Table 5:4)--not withstanding the magnitude and significance levels for these latter correlations. So cub sex ratio--like litter size, whelping level, and cub density--may well actually be positively correlated with food supply and nutrient-energy balance prenatally and circumnatally, as well as postnatally.

Data on cub sex ratio was available from only 9 of the 12 years 1959-70. Less than 4% of the annual variance in cub sex ratio during those 9 years is accounted for by variations in food supply and nutrient-energy balance, whether pre-, post-, or circumnatally. If cub sex ratios for the other 3 years are estimated from the relationships between cub density vs. sex ratio (see Table 3:2, p.29; Chapter 3:I.D.2), proportion of the new total variance in cub sex ratio accounted for by food supply and nutrient-energy balance is little affected. Over the full range of possible levels of food supply and nutrient-energy balance, a sigmoid model might best describe the data, since the male fraction of cubs cannot fall below 0% or rise above 100%. However, within the observed range of data, a semi-logarithmic or linear model is adequate. The semi-logarithmic model was chosen since cub sex ratio was high enough during some years for its response to food supply and nutrient-energy balance to have tapered off.

Judging from estimates for densities of male and female cubs each year, most variation in total cub density arose from variations in male cub density; female cub density was more stable (see Chapter 3:I.D.2). Not surprisingly, therefore, correlations between food supply and nutrient-energy balance vs. male cub density approximate the aforementioned correlations vs. total cub density (both sexes) and vs. cub sex ratio. By contrast, because density of female cubs was more stable, it was virtually uncorrelated with any index of food supply and nutrient-energy balance, whether pre-, post-, or circumnatally, during 1959-70.

5:II.B.7. Recruitment and Attrition

Restriction to 1959-70 of data on densities of recruits within each cohort past age 0.5 year obscures their positive relationships to circumnatal food supply and nutrient-energy balance, just as was the case for whelping level and rate, cub density, and cub sex ratio. Nevertheless, the relationships between cohort sizes vs. food supply and nutrient-energy balance can be discerned if one focuses on the correlation coefficients themselves, irregardless of individual magnitude and significance level. Correlations between cohort sizes vs. postnatal food supply and nutrient-energy balance range from as low as 0.352 (P:1t=0.16) for cohort size at age 1.5 years (Figs. 5:8 and 5:9), to as high as 0.766 (P:1t=0.02) for cohort size at age 5.5 years (Table 5:5).

Magnitude of correlation coefficients tends to increase as the cohorts mature. (This is obscured in the case of postnatal FS-NEB because cohort size at age 0.5 manifests the effect of the 1970 (postnatal) datum for FS-NEB, whereas that is not true for older-age classes or for pre- and circumnatal FS-NEB at any age). This trend is clearest when one averages the correlations between cohort sizes vs. indices of food supply and nutrient-energy balance across all 3 indices, as well as across all 3 periods--pre-, post-, and circumnatally. The mean rises from 0.123 at age 0.5 year, to 0.357 at age 1.5, 0.492 at age 2.5, and 0.802 at age 5.5. (Table 5:5).

That increase in strengths and significance of the correlations is not an artifact arising from the decline in number of

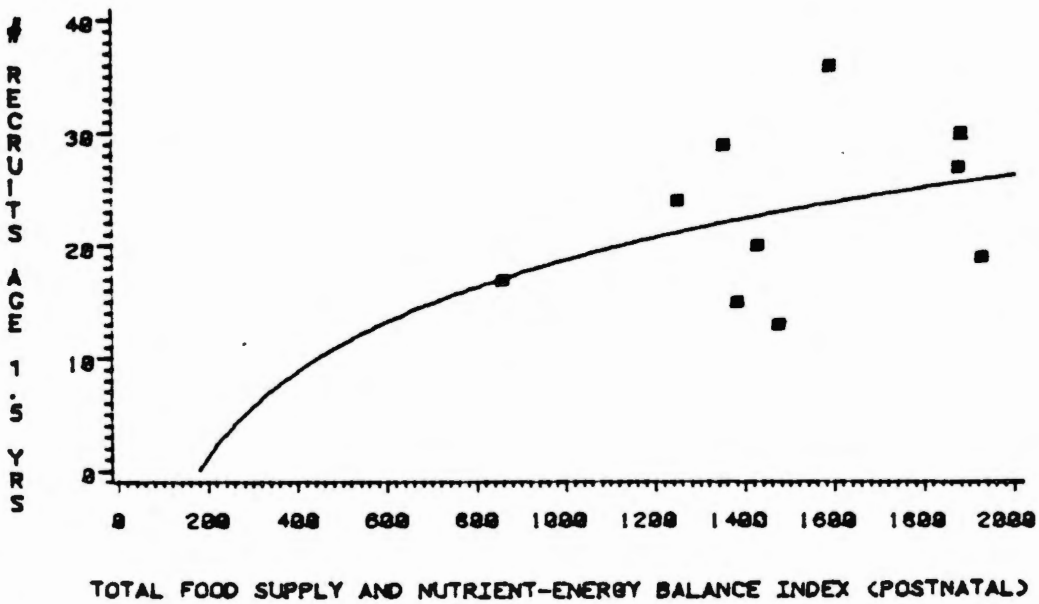


Fig. 5:8. Yearling (1.5 yr) cohort size regressed on the index for for total food supply and nutrient-energy balance postnatally, for Yellowstone grizzlies (1959-70).

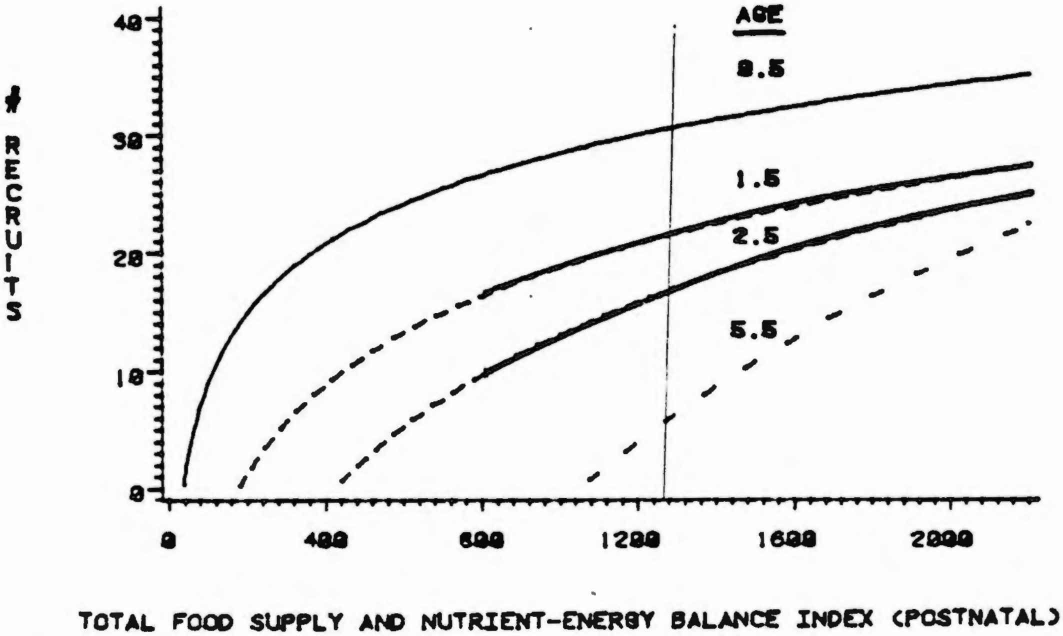


Fig. 5:9. Cohort sizes at ages 0.5-5.5 years regressed on the index for total food supply and nutrient-energy balance postnatally, for Yellowstone grizzlies (1959-70).

cohorts sampled at increasingly older ages (11 at 0.5, 10 at 1.5, 9 at 2.5, and 7 at 5.5). Even when analysis is restricted to the 7 cohorts which could be followed from age 0.5 to 5.5 years, an increase in correlation coefficents is still evident: 0.046 to 0.413 to 0.624 to 0.798.

The increase in correlation coefficents with maturation of the cohort, arises from the fact that both (a) 0.5 year cohort size and (b) recruitment rates over the next five years, were all positively correlated with food supply and nutrient-energy balance at the time each cohort was produced (Table 5:5; Fig. 5:9). The combined responses by reproduction and recruitment to circumnatal food supply and nutrient-energy balance are illustrated by comparing the 1960 vs. 1963 cohorts. For the 1960 cohort, postnatal TFS-NEB was about 860 (i.e., 60 + 800). Sizes of that cohort at ages 0.5, 1.5, and 2.5 years were 35, 17, and 9; corresponding attrition rates were 51% (0.5-1.5) and 47% (1.5-2.5) annually, or 74% (0.5-2.5) overall. By contrast, for the 1963 cohort, postnatal TFS-NEB was about 1880; 0.5 year cohort size was 40 and overall attrition rate to age 2.5 was only 15%.

In Fig. 5:9, recruitment and attrition for a cohort are represented by corresponding points and distances on the vertical line rising from the value of TFS-NEB postnatally for that cohort on the abcissa. Size of an hypothetical cohort at each age--recruitment to that age--is the point where the vertical line intersects the corresponding recruitment curve. Attrition level (#) between successive ages is the distance down that vertical line between the corresponding recruitment curves; division of that distance by cohort size at the younger age yields attrition rate (%).

Since J. Craighead et al. (1974) did not present separate data on the size of each cohort at ages 3.5 and 4.5, the relationships of those cohort sizes to pre- and postnatal food supply and nutrient-energy balances could not be evaluated statistically. The fact that cohort sizes at age 5.5 are also only roughly estimated from the figures for total adults (ages 5.5+; Table 3:2), means that the curve for age 5.5 years is less reliable than those for ages 0.5-2.5.

Semi-logarithmic curves were used to represent cohort sizes and rates of attrition vs. recruitment because they are the simplest models found which provide fits to the data which are (a) statistically "good," (b) consistent among the various parameters, and (c) theoretically reasonable in that they accord with a decline in sensitivity by each parameter to the level of TFS-NEB as that level rises.

The aforementioned results indicate that food supply and nutrient-energy balance (or some closely correlated influence; see Chapter 11:II) affected both 0.5 year size of each cohort and subsequent attrition rate from that cohort at least to age 5.5 years (adulthood), and possibly lifelong. By contrast, food supply and nutrient-energy balance at the time the attrition occurred seem to have had negligible impact (P>0.50)--as though even the lowest levels of food supply and nutrient-energy balance encountered after a bear reached 0.5 year had little effect on its relative probability of either dying or emigrating. But why circumnatal conditions had such a lasting influence, one that apparently was not counteracted by later conditions, can only be speculated (see Chapter 6:IV.B) and will need further investigation. (Indeed, the possibility cannot yet be excluded that this feature is merely an artifact). Like recruitment rate, mean length of interbirth intervals beginning in year t is essentially uncorrelated with indices of food supply and nutrient-energy balance over the next 2 to 3 years, concurrent with the intervals themselves ($r < 0.05$, $P:2t>0.90$).

5:II.B.8. Population Density

Because of the effects of food supply and nutrient-energy balance during the year of a cohort's production on 0.5 year cohort size and its subsequent recruitment, total population density is also positively correlated with food supply during the 3 previous years (t-1 to t-3). Indeed, average food supply and nutrient-energy balance (TFS-NEB) for years t-1 and t-2 accounts for 67% ($P:1t=0.004$) of the variance in population density in each year t during 1959-70 (Fig. 5:10).

5:II.C. Body Weight vs. Food Supply

Knight et al. (1981) reported that 3 grizzlies which fed at the Cooke City dump from at least 1975 until its closure in 1980, all weighed less after closure. Furthermore, mean weight of males which

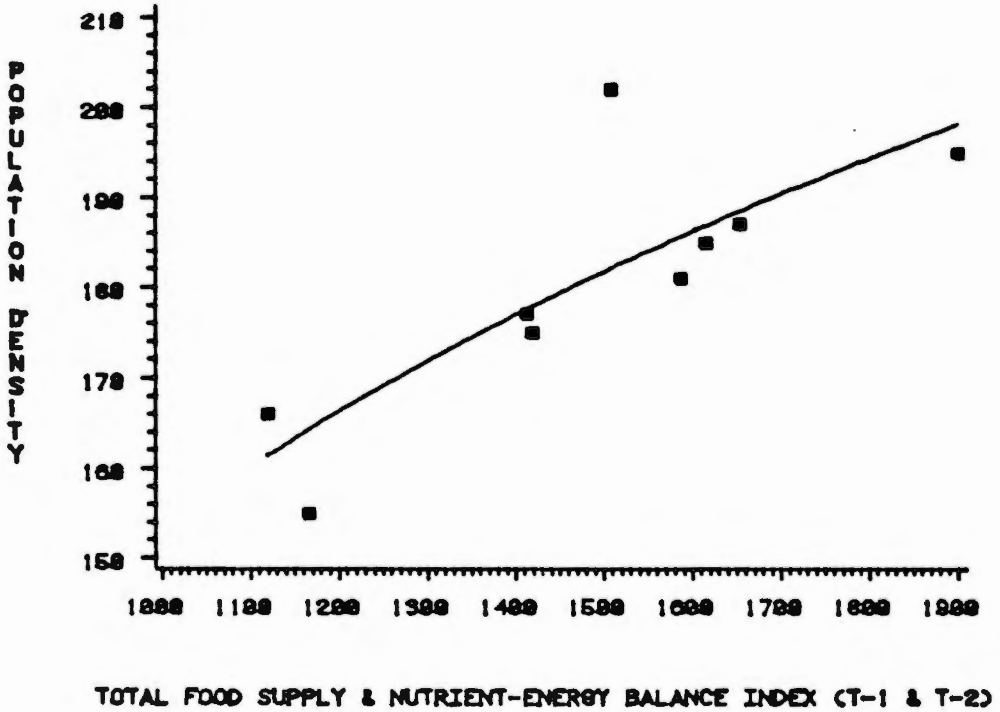


Fig. 5:10. Population size each year regressed on the index for total food supply and nutrient-energy balance during the 2 previous years, for Yellowstone grizzlies (1959-70).

used that dump was significantly (P:2t<0.05) heavier than the mean for males without access to garbage, although weights of females from the 2 groups did not differ significantly. The largest male marked up through 1980 was one which fed at the Cooke City dump. He was about 50 Kg heavier than the largest male not feeding on garbage, one which supplemented his diet of natural forage by eating domestic livestock, and about 125 Kg heavier than the average adult male feeding exclusively on natural foods.

There is also basis for testing whether body sizes of Yellowstone grizzlies were smaller after closure of the Park dumps than when garbage was abundant. Body weight data have been published for 1959-70 by J. Craighead et al. (1982a) and for 1974-80 by Knight et al. (1981); so the 2 data sets (Table 4:5, p.87) represent body weights prior to vs. after _completion_ of dump closure. Those authors did not publish their data in sufficient detail for a reviewer to calculate standard deviations. So any comparison between the means for weight data before vs. after closure ended, has to be done without tests for statistical significance of the differences.

Sampled cubs (median age 0.5 year) weighed about the same before vs. after closure. But yearlings and 2-year-olds sampled after closure were about 6% _heavier_ than those sampled before closure. Even _if_ that apparent increase in heaviness is a sampling artifact, it strengthens the impression that juveniles, like cubs, were not _lighter_ after closure than before. By contrast, sampled adult (≥5-year-old) females and males were, respectively, 16% and 25% lighter after closure. Pre- vs. post-closure weight differences for subadults (3&4-year-olds) were intermediate.

The difference in adult body weights pre- vs. post-closure presumably reflects the declines in food supply and nutrient-energy balance due to closure and to worsening climate. Whether it also reflects any systematic sampling bias isn't known to me. Without data on the date when each bear was weighed, and its age then, one cannot estimate the extent to which the apparent weight changes between the periods might represent a sampling bias rather than dump closure and climatic worsening. For example, were adults weighed by J. Craighead et al. (1982) more mature, on average, than those weighed by Knight et al. (1981)? If so, then part of the difference in mean weights of adults before vs. after dump closure could be attributed to sampling error rather than to closure per se.

5:II.D. Maturation Rate vs. Food Supply

For the 1959-70 period, J. Craighead et al. reported ages at first whelping for 16 females, averaging 5.8 ± 1.2 years. By contrast, the mean and standard deviation for females observed by Knight et al. (1981) during 1974-80 were 6.2 ± 1.0; that is an increase of 0.4 year (P:1t=0.19). Although sample size is too small for this apparent 6% decrease in maturation rate to be statistically reliable, it is consistent with evidence that most other reproductive parameters and body weights of adults declined between the 1960's and the 1970's, apparently as a consequence of dump closure and worsening climate. Furthermore, as shown above in Section I.A. and later in Chapter 6:III., negative correlations between generation length vs. food supply and body weight are typical across bear populations; the same is true in other mammals (Stringham, in prep.).

5:III. SUMMARY

5:III.A. Comparison Among Populations

1) Like adult body weights, litter size, productivity (C/L/IBI), reproductive vigor (net effects of reproductive rate on population growth rate), and indices of maturation rate to weaning and to puberty, are all negatively correlated with latitude. This is probably attributable to (a) the decline in primary productivity at higher latitudes, as well as (b) the longer, harsher winters, and higher energetic costs of thermoregulation there.

2) Also like adult body weights, litter size, productivity, reproductive vigor, and indices of maturation rate for grizzlies tend to be higher at the coasts of Alaska than at inland habitats in Alaska and northern Canada. Not only are conditions milder at coasts than inland, but these particular coastal populations are at lower latitudes than the inland populations. Furthermore, some important foods (e.g., salmon or marine mammal carrion) are typically more abundant on the coasts even at comparable latitudes.

5:III.B. Comparison Among Years within Populations

1) Picton (1978) devised an index of climatic severity based on mean precipitation and temperature for Yellowstone National Park (YNP) during October-May. Climatic fluctuation statistically accounted for 43% of variance in mean annual litter sizes for YNP grizzlies during 1959-76, based on the reproductive data of Craighead et al. (1974), Cole (1974), and Knight et al. (1977).

2) Since before 1900, until the late 1960's, YNP grizzlies have supplemented their diets of natural foods with garbage consumed at dumps within or adjacent to YNP. For instance, during 1959-61, there was an estimated 60 Kg per day of edible garbage potentially available per grizzly observed at the YNP dumps, although it is not known what proportion of this was actually consumed by the bears, or how nutritious it was. In any event, garbage was obviously a major food source. Between 1968-71, access to most of this garbage was progressively eliminated, thereby presumably reducing carrying capacity of YNP for grizzlies.

3) Closure of the dumps was associated with a substantial decline in reproduction. as documented by J. Craighead et al. (1974), Cole (1974), and Knight et al. (1981, 1982). Litter size declined about 19%; numbers of cub litters and of cubs per year-class cohort declined about 16% and 29%, respectively. Maturation rate apparently declined 6%. Body weights of adults and subadults declined up to 25%. Weights of unweaned young did not decline; in fact, weights of 1- and

2-year-olds seems to have increased. Possible explanations for those increases are considered in Chapter 6:VIII.

4) Analyses presented here indicate that dump closure accounted for about 70% of that decline in litter size; the remainder was accounted for by a coincidental worsening of climate, judging from Picton's index. Respective impacts of dump closure on other parameters of reproduction and recruitment were probably comparable; but available data do not suffice for verifying that. Impacts by dump closure might have resulted from (a) the consequent elimination of that source of food, (b) from increased social strife arizing from greater contest competition for the remaining food, and (c) increased attrition rate due to removal of grizzlies by humans (mainly to protect people or property). These latter hypotheses are discussed in Chapters 6:IX and 9:II.

5) In lieu of actual data on the supply of edible garbage available to YNP grizzlies, that supply was estimated by assuming that it was directly proportional to number of visitors to YNP each summer. Picton's (1978) climate index was used as an index of natural food supply and nutrient-energy balance. Once the garbage supply and climate indices were put into equivalent units, they were combined to provide an index for total food supply and nutrient-energy balance. That, in combination with demographic data, enables one to estimate food supply per bear and per unit bear-mass. Of these, supply per unit bear-mass was the best predictor for rates of reproduction and recruitment -- as might be expected, since it is presumably the best

index of individual nutrient-energy balance. Body weights specific to each season and age-sex class might have provided an even better index; but such data weren't available on an annual basis.

6) For Yellowstone grizzlies, litter size was positively linearly proportional to all indices for food supply and nutrient-energy balance (total supply, supply per bear, and supply per unit bear mass). That is, litter size was equally sensitive to a change in the level of food supply and nutrient-energy balance at any observed level--although sensitivity probably declines at levels substantially higher and lower than those observed during 1959-81. It is logically impossible for litter size to fall below 1 C/L, and unlikely for mean litter size to rise above about 3 C/L, since that exceeds any mean yet recorded in any other population.

By contrast, even within the range of food supply and nutrient-energy balance levels observed, sensitivities by densities of cubs and of adult females whelping each year, were inversely related to the average level of food supply and nutrient-energy balance. The same was found for whelping rate in Smoky Mountains black bears (see Eiler 1981) and in reindeer (Reimers 1983).

In other words, when food supply and nutrient-energy balance were low, (a) mean litter size for females which succeeded in whelping and in rearing litters to at least age 0.5 year, was affected much less than (b) the density and proportion of adult females that succeeded. By contrast, even when food supply and nutrient-energy balance were so high that most females succeeded in whelping and rearing at least 1 cub to age 0.5 year, litter size was still affected by variations in food supply and nutrient-energy balance.

Sensitivities of (a) interbirth interval and (b) recruitment from infancy to adulthood, to variations in the level of food supply and nutrient-energy balance, were also inversely related to the average level.

Whereas the relationships between some of these parameters vs. food supply and nutrient-energy balance appear approximately semi-logarithmic, those for rates of whelping and attrition should be asymptotic. More data at high and low levels of food supply and nutrient-energy balance will be needed to confirm whether or not these are the best kinds of models for each parameter. For instance, sigmoid models which rise more gradually from their lower limit (e.g., the abcissa) might be more realistic for some of them, including cub litter size and sex ratio.

7) As those results reveal, essentially all of the parameters of reproduction and recruitment tested are positively correlated with the indices for food supply and nutrient-energy balance, pre-, post-, or/and circumnatally. Two possible exceptions in the case of Yellowstone grizzlies are whelping rate (proportion of adult females whelping each year) and cub sex ratio. There is good reason to believe that the apparently weak or non-existent correlation between whelping rate vs. level of food supply and nutrient-energy balance is just an artifact of having data only when the level of FS-NEB was so high that it had little affect on whelping rate (1959-70).

Furthermore, since most variation in cub sex ratio and in cub density was due to variation in male cub density, and because of the clear positive correlation between cub density vs. food supply and nutrient-energy balance during 1959-81, cub sex ratio may have also been positively correlated with the level of FS-NEB. But here too, this cannot be confirmed until more data become available on cub sex ratio at low levels of food supply and nutrient-energy balance.

CHAPTER 6

DISCUSSION

6:I. INDICES OF FOOD SUPPLY AND NUTRIENT-ENERGY BALANCE

Lacking direct data on food supply and nutrient-energy balance for YNP grizzlies, 2 indices were used as surrogates. That was done in the hope that the indices would be highly enough correlated with food supply and nutrient-energy balance to provide at least preliminary quantitative models for the relationships between rates of reproduction and recruitment vs. food supply and nutrient-energy balance. The high correlation (r = 0.988) between monthly variations in density of grizzlies using YNP dumps vs. the garbage supply index suggest that this index does indeed correspond well with garbage supply. So too, correlations between both the garbage and climate indices vs. parameters of reproduction and recruitment (Stringham, in prep.) and vs. body weight and generation length (before vs. after dump closure) further substantiate the validity of these indices as surrogates for direct measures of supplies of manmade and natural foods and for nutrient-energy balance.

The utility of Picton's climate index is self evident. But its interpretation is not. Although there is little doubt but that winter snowfall and temperature do affect both energetic costs of thermoregulation and food supply, the exact manner in which they do so is puzzling.

Picton (1978) suggested that cold weather increases costs of thermoregulation, whereas greater snow depth, providing greater thermal insulation, would ameliorate colder weather. Without data on correlations between snow depth vs. temperature, and on insulative qualities of snow per unit depth, the effects of winter severity on thermoregulation by bears remain obscure.

So too, effects of winter severity on food availability seem contradictory. (1) Early snows in autumn could decrease current availability of food, such as pine nuts; but a proportion of those nuts are again available and probably nutritious after snow melt during the following spring (J. Craighead, pers. comm.). (2) Prolongation of snow pack in potential feeding areas during spring would delay availability of new plant growth for food. Yet, prolongation of snow pack at altitudes above feeding areas might increase availability of moisture to food plants during otherwise dry summers. (3) Picton's index extends only from October (or September) to May. Yet, "summer weather affects the [pine] nut crops and also has a direct bearing on the next year's grass and forb production" (J. Craighead, pers. comm.). (4) Severe winters apparently increase mortality of wapiti, bison, and other ungulates in YNP, thereby increasing availability of carrion in spring, before nutritious plant food is available in abundance. The relative importance of different foods for YNP grizzlies has been analyzed by Mealey (1975, 1980) and by Knight et al. (1980, 1981).

The positive correlations between litter size and other reproductive parameters vs. climate index (Picton 1978; Stringham, in prep.) suggest that the detrimental effects of especially severe winters outweigh the beneficial effects. However, detailed interpretation of the relationship between the climate index vs. food supply and nutrient-energy balance and vs. reproduction and recruitment has to await collection of the data needed for determining the relative importance of effects by various climatic factors--snowfall, standing snow depth, mean temperature, or extremes of temperature--on either thermoregulation during hibernation or on food supply before vs. after hibernation.

Another reason for caution in interpretation of Picton's climate index is that it is based only on data from the Mammoth weather station, near the northern border of YNP. Southern parts of YNP are largely under the influence of another weather system. Two major systems converge in YNP, and data are available from only 1 of them. Although climatic data has also been collected from other areas of YNP, it is not complete enough or thorough enough to support this kind of analysis (Picton, pers. comm.).

Climate indices such as Picton's are intruiging as indicators for gross ecosystem status, potentially applicable to many of the species within each ecosystem. For example, Picton's index has had applicability not only to grizzlies, but also to mule deer and wapiti (Picton 1979; Houston 1982). How applicable that approach will be to other ecosystems and biomes remains to be determined. Certainly, it should be tried. As Picton demonstrated, even in cases where data on food supply is not available (or is simply categorized as abundant vs. scarce), ratio-scaled climatic data might provided added insight. However, the number of causal "steps" from climate to nutrient-energy balance for bears or other large mammals is so great and complex that climate indices may be good predictors of dynamics only under specialized conditions.

In any event, climatic indices for food supply and nutrient-energy balance clearly leave something to be desired as the basis for analyzing and predicting rates of reproduction and recruitment, and thus for modeling population dynamics. Of potentially even greater value will be the actual measurements for abundance of major foods (e.g., hard mast, berries, salmon, seals, or carrion) being made by some investigators (e.g., Jonkel & Cowan 1971; Stirling & Smith 1976; Picton 1978; Eiler 1981; Knight et al. 1981, 1982), particularly if these measurements are accompanied by assessment as to how much of that food is actually obtained by bears (or other focal species), and to how nutritious it is (see Mealey 1975, 1980; Bunnell 1983).

Calculation of amounts of food per bear and per unit bear mass provides rough estimates of nutrient-energy balance. Even better might be data on body weight or size. Yet, even that data has limited utility. For it is presumably not total body weight (mass) per se, but lean body mass, fat mass, fat:lean ratio, or related physiological parameters that actually govern rates of ovulation, implantation, etc.

(Sonic probes or other methods developed for assessing subcutaneous fat depths for livestock or humans might have applicability to bears or other wildlife.) For a given body weight, small fat females might have different rates of reproductive success than large lean ones. The average body weight or size critical for attaining or maintaining reproductive competence might differ from one population to another within each bear species, and certainly among species. Perhaps some more specific physiological parameter (e.g., fat:lean ratio, kidney-fat index, or blood profiles) will be more consistently correlated with reproduction and recruitment rates than is total body weight or size, and will thus serve better as a basis for comparison among populations and species, and for prediction.

Whatever the relative superiority of indices on each of these 3 levels--climate vs. specific food supplies vs. body weight or nutrient-energy balance--use of indices on all 3 levels should provide even greater insight and predictive power than would indices on any single level.

6:II. RATES OF REPRODUCTION AND RECRUITMENT RELATIVE TO LATITUDE AND LONGITUDE

6:I.A. Latitude

Results in Chapter 5 of comparison among grizzly populations reveal negative correlations between latitude vs. reproductive parameters: maturation rates to weaning and to puberty, cub litter size, productivity, and reproductive vigor. That is consistent with what Rausch (1961) suggested for maturation rate in black bears and what Bunnell & Tait (1981) found for litter size in polar bears. These correlations are attributed primarily to the effect of latitude on nutrient-energy balance of the bears, as discussed in Chapter 4:III.B. This is substantiated by the latitudinal gradient in body weights. To further test this interpretation, one might regress rates of reproduction and recruitment vs. climatic data per se. Among the variables which might be considered are: annual precipitation and mean annual (e.g., winter) temperature, as Picton did, as well as mean annual low temperature, number of days below freezing or with snow cover, average snow depth and density, or insolation and albedo.

The relationship between mean body weight vs. latitude might be influenced not only by (a) the effects of primary productivity and direct nutient-energy costs of living favoring small body size, but also by (b) the contradictory cold climate selection pressures favoring low surface-volume ratio, and thus large body size. In other words, the latitude-dependent effect of food supply on body weight might be weaker than effects of comparable variations in food supply among habitats where climate does not vary substantially.

6:I.B. Longitude

Reynolds & Beecham (1980), Bunnell & Tait (1981), and others have remarked on differences in productivity by populations to the west vs. east of 95 degrees west longitude in North America. As can be discerned from data in Table 6:1, populations in the West (Montana

Table 6:1. Reproductive parameters (mean values) for wild populations and captive black and polar bears.*

Longitude and Population	Generation Length (G)	Interbirth Interval (IBI)	Litter Size (C/L)	Productivity** (C/L/IBI) (= Pr)	Fecundity* Pr*%FC	Reproductive** Vigor (RIV)
URSUS AMERICANUS American Black						
Western						
Montana[1]	≥7.3**	3.85	1.7	0.44	0.200	≤-5.00
Idaho Council[2]	4.75**	3.23	1.9	0.59	0.268	-1.00
Lowell[3]	5.0**	3**	1.65	0.55	0.250	-2.00
Eastern						
Minnesota[4]	5.2**	2.44**	2.70**	1.11	0.498	+4.46
North Carolina[5]	4**	2**	2.39**	1.20	0.546	+7.00
Smoky Mountains[6] (North Carolina and Tennessee)	5**	2.38	2.5 (2.36)	1.05 (0.99)	0.473 (0.446)	+4.03 (+3.47)
Pennsylvania[7]	3.6**	2	2.9	1.45	0.660	+10.80
Captives[8]	4	2***	2.4	1.20	0.546	+7.00

Table 6:1. (Continued)

Longitude and Population	Generation Length (G)	Interbirth Interval (IBI)	Litter Size (C/L)	Productivity** (C/L/IBI) (= Pr)	Fecundity* Pr*%FC	Reproductive** Vigor (RIV)
<u>URSUS MARITIMUS</u> <u>Polar Bears</u>						
Spitsbergen[9]	4	2.18*	1.67	0.77	0.385	+3.10
Eastern[10] Beaufort Sea	≥4.96	3.03*	1.68	0.55	0.275	≤-1.08
Alaska[11]	5.44	3.6	1.58	0.44	0.220	-3.03
Captives[12]	4-6	2.1***	1.64****	0.78	0.390	+2.20***

* After Stringham (1980:Table 2) and Bunnell & Tait (1981:Table 3).

** Results of calculations from data provided by author.

*** Interbirth intervals for captives, and thus their per capita productivity and reproductive vigor may ave been altered by keepers who separated neonates from their mother before she would have weaned them from lactation. This seems to be particularly common with polar bears, since mothers of this species are typically unsuccessful in rearing young in captivity.

**** Even mean litter siz for captive polar bears may be a minimum figure due to loss of some cubs before they could be counted; consumption of young by the mother is much more common in polar bears than in either grizzly or black bears.

and Idaho) tend to have mean generation lengths at least 5 years long, whereas in the East (Minnesota, the Great Smoky Mountains, North Carolina, and Pennsylvania) they tend to be no more than about 5 years. A similar difference is seen for interbirth intervals. They are typically 3 to 4 years in the West; by contrast, in the East, they seldom reach 3 years except during temporary famines, and the average is closer to 2 years. So too, mean litter sizes tend to be under 2.0 in the West, but over 2.3 in the East.

Bunnell & Tait (1981) also reviewed data showing corresponding differences between eastern vs. western populations in body weights of adult females. According to my calculations from that data (Table 6:2): (1) For western populations, 52 adult females averaged 64 Kg, compared to 90 Kg for 90 eastern females (P:2t = 0.0005; sample-size-weighted and -unweighted means are the same). (2) For males, the means for western vs. eastern populations are 92 Kg vs. 138 Kg, respectively (P:2t = 0.001). (3) When data for males and females in each population are combined and averaged (unweighted) to minimize effects of sampling bias, the means (for males and females together) are respectively 78 Kg in the West vs. 114 Kg in the East (P:2t = 0.0002). So, even though the weight data does not all come from the same populations as the reproductive data, there do seem to be corresponding longitudinal gradients in both weight and productivity for black bears. (Sample sizes for the t-tests were number of populations, not number of bears).

Table 6:2. Body weights for adult black bears in western vs. eastern zones of North America.*

Longitudinal Zone & Population	Weight (Kg)**			
	Male	Female	Unweighted Mean	Ratio M/F
WESTERN				
Alberta	82	74	78.0	1.1
(Nagy & Russell 1978)	(20)	(16)		
Washington	87	58	72.5	1.5
(Poelker & Hartwell 1973)	(18)	(17)		
California	98	58	78.0	1.7
(Piekielek & Burton 1975)	(30)	(11)		
Montana	102	68	85.0	1.5
(Jonkel & Cowan 1971)	(5)	(8)		
EASTERN				
New York	147	91	119.0	1.6
(Harlow 1961)	(49)	(19)		
New York	165	99	132.0	1.7
(Black 1958)	(25)	(16)		
New York	136	85	110.5	1.6
(Sauer 1975)	(43)	(24)		
New Hampshire	120	83	101.5	1.4
(Harlow 1961)	(19)	(11)		
Florida	139	86	112.5	1.6
(Harlow 1961)	(16)	(12)		
Michigan	124	95	109.5	1.3
(Erickson & Nellor 1964)	(4)	(8)		
MEAN (unweighted)				1.5

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* Values given are mean and sample size (n); after Bunnell & Tait 1981:Table 1.

** Fall (September-November) weights selected to increase comparability.

These longitudinal gradients are usually attributed to the greater availability in the East of mast and other high energy foods. However, no one has yet published a formal test of that assertion, for instance in the form of a comparison of data on differences in food supply, climate, or nutrient-energy balance. Note that Montana and Idaho are the farthest west for which we have comprehensive data on reproductive rates. Weight data are available from Poelker & Hartwell (1973) for Washington state and from Piekielek & Burton (1975) for California; these data indicate that average size of bears are as small close to the Pacific Coast as in the Rocky Mountains. However, I have not been able to find enough data to (a) discern whether those particular western black bears had access to abundant salmon, mast, or other rich foods, and whether those that do are as large as eastern black bears.

Although substantiating evidence has not yet been gleened from existing data sets, it seems likely that some of this latitudinal and longitudinal variation in productivity is not just facultative, but genetically determined. We need to find out, for example, whether for a given body weight, black bear females in the eastern deciduous forests tend to be any more or less productive than equal-sized females in the western spurce-fir forests or on the Pacific coast. The eastern females may typically have more resources to spare for reproduction. Similar questions apply to comparison among bear populations on the basis of latitude or habitat type (e.g., coastal vs. inland).

6:III. RATES OF GROWTH, MATURATION, AND WHELPING

6:III.A.. Growth Rate

Growth in bears, as in most mammals, rises rapidly after birth, gradually slows, and may eventually plateau at some maximum average size. This plateauing is more abrupt for females than for males in grizzly and black bears (Rausch 1961; Jonkel & Cowan 1971; Pearson 1975; Glenn 1980; Beecham 1980b; Knight et al. 1981; Eiler 1981; Craighead & Mitchell 1982). That is consistent with data on other mammals, including Margay cats (Peterson & Peterson 1978), mink (Stout et al. 1963), silver fox, blue fox (Aitken 1963), and swine (Anderson 1974).

For black bears, rate of growth to adulthood and mean weight maintained as adults are directly related to nutritional status. Wild bears subsisting primarily on natural diets tend to reach normal adult weight later and to maintain a lower maximum than (a) wild bears supplementing their diets with substantial amounts of manmade foods (e.g., garbage) and (b) well-fed captives. (Rausch 1961; Rogers 1976, 1977; Eiler 1981). However, in exceptionally good habitats, wild bears on primarily natural diets are as large as those in captivity receiving abundant manmade foods (Alt, pers. comm.). Rogers et al. (1976) reported that black bears captured at dumps were substantially larger than same-aged bears captured in campgrounds and residential areas. This was attributed to the greater abundance of garbage at dumps, implying that better-fed bears grow larger. They did not discuss the role of body size in competing for access to the garbage; larger bears may have excluded smaller ones from the dumps.

6:III.B. Maturation Rate vs. Growth Rate

At least for black bears, rate of maturation--probably to weaning and certainly to puberty--is directly related to rate of growth and to food supply for the individual and the population (Rausch 1961; Rogers 1976, 1977; Fig. 6:1). This is consistent with the above-mentioned correspondence between growth rate vs. nutrient-energy balance in bears, as is also true for other mammals (Sadlier 1969; Stringham, in prep).

Beecham (1980a,b) compared maturation rates between 2 black bear populations in Idaho. In that where growth was faster (but maximum body size not larger), females reached puberty at a younger age (4.25 vs. 4.50 years). Beecham attributed these differences in rates of growth and maturation to corresponding differences in habitat quality, presumably in terms of food supply and nutrient-energy balance. Rogers (1983) compared data on black bears in Montana (Jonkel & Cowan 1971) and Pennsylvania (Alt 1980; Kordek & Lindzey 1980) with his own data from Minnesota on body sizes of cubs in the fall vs. ages at first whelping by females. In Montana and Minnesota, fall weights of cubs were only about 20 Kg, whereas those in

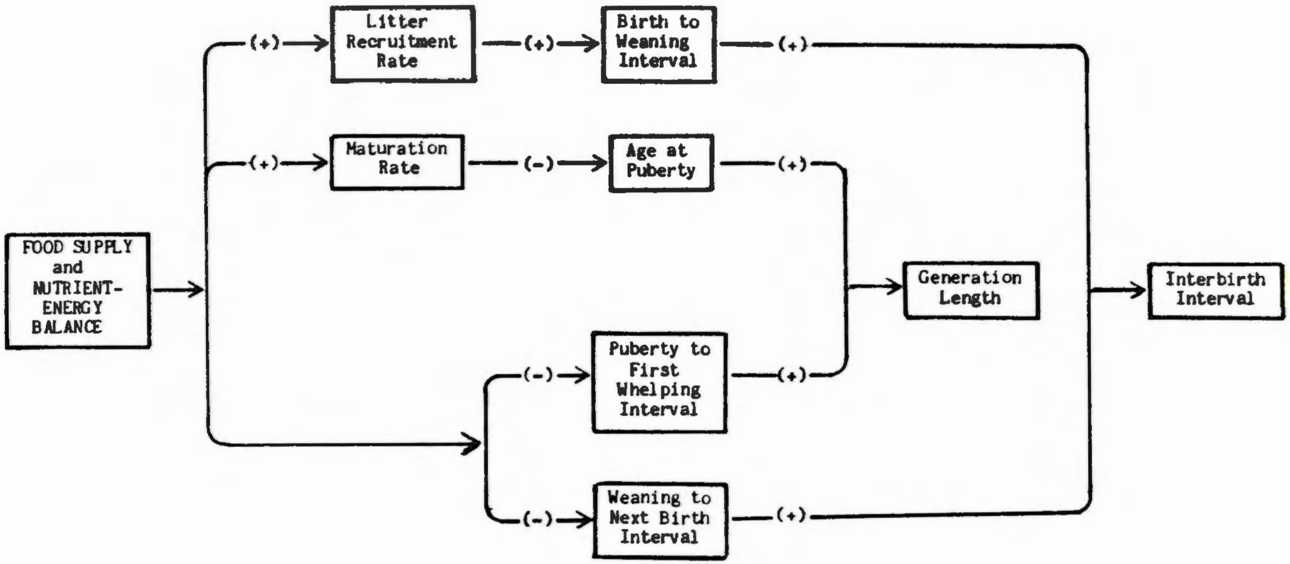

Fig. 6:1. Maturation rate, interbirth interval, and generation length, correlated to food supply and nutrient-energy balance. Each sign (+ or -) refers to a correlation.

Pennsylvania were twice that heavy. Ages at first whelping averaged about 7.3 years in Montana and 6.3 years in Minnesota, compared to about 3.5 years in Pennsylvania (Table 6:1).

According to Eiler (1981), both Sadlier (1969) and Hafez (1968) have reviewed data for various mammals indicating that puberty and/or first reproduction for a female are delayed until her growth rate declines and weight _begins_ to plateau. So too, correspondences between (a) initial attainment of adult weight and/or (b) subsequent maintenance of some minimum weight vs. attainment or maintenance of reproductive competence by female bears have been documented by Rogers (1976, 1977, 1983), Beecham (1980b), Eiler (1981), and others. They found that both nulliparous adolescent and multiparous females may mate even during years when food supply is poor. But of those which are still lean when hibernation begins, few are found with cub litters during the following spring or summer. This coincides with earlier findings on black bears by Jonkel & Cowan (1971) and on grizzlies by J. Craighead et al. (1969, 1974) that some females first mated 1 or more years before they succeeded in conceiving litters that survived long enough to be censused (postnatally). Since these females may not even have succeeded in conceiving, the phenomenon is sometimes called "premature estrus" (see Section III.C.4, below).

6:III.C. _Whelping Level and Rate_

Jonkel & Cowan (1971) presented evidence that, among Montana black bears, whelping rate was correlated with huckleberry (_Vaccinium_ spp.) production during the previous autumn. Using the quantification scores for their abundance categories described in Chapter 4:III, the correlation between mean annual berry production vs. proportion of marked adult females seen with cubs during the following summer is 0.712 (P:1t=0.02, n=8) by the Pearson product-moment method and 0.744 by the Spearman rank method. Jonkel & Cowan also reported that cubs of females with territories at higher altitudes, where food seemed less abundant, tended to grow more slowly and were more likely to be nursed as yearlings--which could inhibit estrus and thereby lengthen interbirth interval by an extra year for the dam, compared to females at lower altitudes.

Similarly, among Minnesota black bears, whelping level and especially whelping rate were higher in springs after summer-fall seasons with abundant food than after seasons with scarce food (Rogers 1976, 1977, 1983). (Fig. 6:2). Corresponding Student-t values and Pearson correlation coefficients are

#L: T = 2.4, r = 0.695, P:1t = 0.03, n=8
#L/AdF: T = 3.5, r = 0.818, P:1t = 0.007, n=8

where food supply categories were treated as dummy variables for calculation of Pearson correlation coefficients (Chapter 4:III; Table 6:3). Rogers (1977, 1983) also provides details about relationships between body weights of females $\geq$3.5 years old vs. their whelping rate during the following spring: 0% of 17 females weighing <67 Kg, 94% of 34 females weighting >80 Kg, and 29% of 14 females with intermediate weights; survivorship of these latter litters was correspondingly

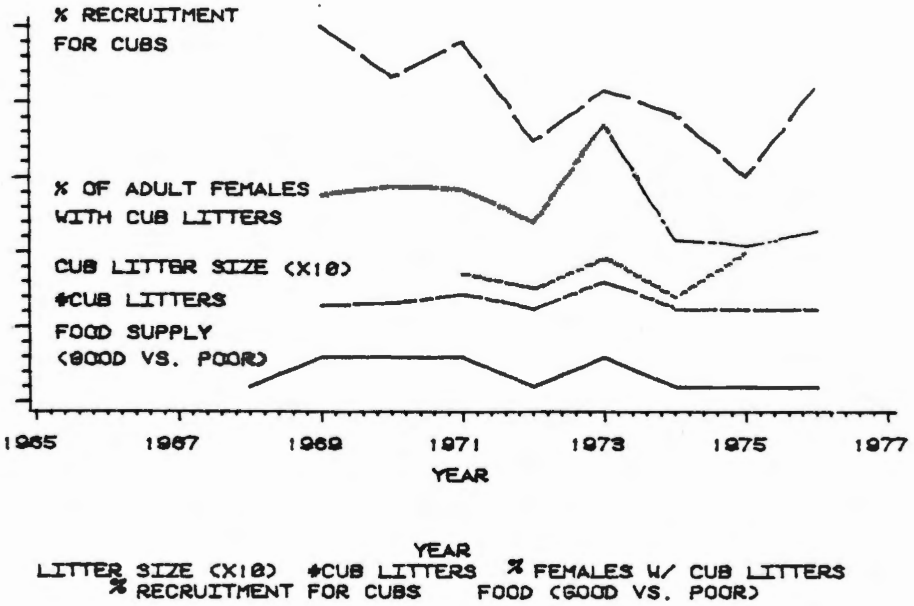

Fig. 6:2. Reproductive and recruitment parameters regressed on the food supply index (good vs. poor) for Minnesota black bears (data from Rogers 1977).

Table 6:3. Parameters of reproduction and recruitment regressed on food supply for Minnesota black bears.*

Parameter	t	r	P:1t	n	Regression Equation	Developmental Period**
Cub litter size [R][1]	-2.35	-0.805	0.95	5	C/L = 2.98 - 0.106*FS	prenatal
	+0.66	+0.354	0.28	5	= 2.92 - 0.046*FS	postnatal
Whelping level [R+N]	+2.37	+0.695	0.03	8	#L = 8.12 + 0.425*FS	prenatal
	-0.95	-0.392	0.81	7	= 8.25 - 0.250*FS	postnatal
Whelping rate [R+N]	+3.48	+0.818	0.007	8	#L/AdF = 41.0 + 2.05*FS	prenatal
	-0.04	-0.019	0.52	7	FS	postnatal
% Male cubs [R]	-0.12	-0.069	0.55	5	FS	prenatal
	-0.12	-0.070	0.55	5	FS	postnatal
Cub density [R]	-0.29	-0.167	0.61	5	FS	prenatal
	-1.55	-0.667	0.89	5	#C = 14.3 - 0.0667*FS	postnatal
% Recruitment rate ages 0.5-1.5 [R+N]	+0.02	+0.008	0.49	8	FS	prenatal
	+2.82	+0.755	0.015	8	%R = 77.6 + 2.32*FS	postnatal

* Values given are the Student t-test statistic (t), the Pearson correlation coefficient (r), probability that the means were not higher when food was abundant than when it was scarce, and thus that the correlation was not positive (P:1t), and sample size (n). All were calculated from data provided by Rogers 1977, as shown in Tables 3:3 and 3:8).

** Developmental period during which food supply (or nutrient- energy development affects the parameter of reproduction or recruitment.

[1] R = resident
N = non-resident; see Table 3:3 for explanation.

poorer and/or initial size of the litters smaller than for litters produced by the heavier dams.

The relationships between whelping level and rate vs. food supply or nutrient-energy balance or body weight are further revealed by data for which the food supply has been quantified on a ratio scale--data for Yellowstone grizzlies and Smoky Mountains black bears. (Table 6:4). Recall that whelping level and rate are little affected by changes in the level of food supply and nutrient-energy balance when the average level is high, but strongly affected when the average level is low. That is also consistent with the asymptotic rise in pregnancy rate with increasing body weight found for reindeer by Reimers (1983).

6:III.C.1. Pregnancy Rate vs. Delayed Implantation

Data from Rogers (1976, 1977, 1983) and Eiler (1981) on neonatal black bear litters indicates that if the decline in whelping rate during springs after autumn famines was due to postnatal mortality of litters, the deaths must have occurred within the natal den, probably within the first 1 or 2 months postpartum. Rogers considers that unlikely, favoring instead the possibility of failure to implant; or, fetuses might be lost by resorption or abortion.

Implantation normally occurs in late November or early December, near the beginning of hibernation (Hamlett 1935; Dittrich & Kronberger 1963; Wimsatt 1963; Erickson 1964; J. Craighead et al. 1969; Foresman & Daniel 1983). Implantation during autumn is also

Table 6:4. Demographic parameters correlated (+ or -) with annual variations in indices for food supply or nutrient-energy balance pre-, post-, or circumnatally in several bear popuations.*

Species & Population	Developmental[1] Period	Litter Size	Whelping[2] Rate (%)	Productivity C/L/IBI	Cub Litter Weight	Cub Density	Cub Recruitment Rate (%)	Yearling Recruitment Rate (%)
U. ARCTOS Grizzly Bear								
Yellowstone National Park								
(Picton 1978)	Prenatal	+[3]						
(Stringham)	Prenatal	+	+			+	+	+
	Postnatal	+	+			+	+	+
	Circumnatal	+	+			+	+	+
U. AMERICANUS Black Bears								
Alaska (Hatler 1967)	Prenatal	+						
Montana (Jonkel & Cowan 1971)	Prenatal		+					
Minnesota[4]	Prenatal	-	+		+		+	
(Rogers 1976,	Postnatal	+	+				+	+
1977)	Circumnatal		+				+	

Table 6:4. (Continued)

Species & Population	Developmental Period	Litter Size	Whelping Rate (%)	Productivity C/L/IBI	Cub Litter Weight	Cub Density	Cub Recruitment Rate (%)	Yearling Recruitment Rate (%)
U. AMERICANUS Black Bear								
Great Smoky Mountains (Eiler 1981)	Prenatal	+	+					
U. MARITIMUS Polar Bear								
Canadian Arctic (Stirling et al. 1976; Stirling & Smith 1976; Bunnell & Tait 1981)	?	+[5]	+[2]	+			+	+

* Each parameter was assessed by age 0.5 year unless otherwise specified.

[1] Period when food supply or nutrient-energy balance estimated mean for population or for dams) was assessed. In this Table, "circumnatal" implies that both pre- and postnatal periods were found important; "?" implies that either or both of those periods is important, but which was not determined.

Table 6:4. (Continued)

[2] Proportion of adult females with litters. For YNP grizzlies this is the proportion of all adult females in the population; for GSMNP black bears it is proportion of all "fertile" females (see text). For Canadian polar bears, it is proportion of adult females with litters of any age, most less than 2.5 years old.

[3] Sign of correlation (+ or -). It is only for the Yellowstone, Minnesota, Montana, and Canadian bears that sample sizes are large enough to support calculation of coefficients for correltion and significance. Although data from the various studies cannot be formally pooled, in order to provide a more reasonable sample size, overall there is great consistency of the positive correlations between various parameters of reproduction and recruitment vs. indices for food supply or nutrient-energy balance in bears and in various other mammals. The only contradictory result was the negative correlation obtained by by calculations from Rogers' data for cub litter size vs. prenatal food supply (see text for details).

[4] Correlations found by analysis of data provided by the author.

[5] The correlation for litter size was non-significant even if real, it was minor compared to responses by the other parameters to variations in food supply (see text). It is not clear from information provided by the authors whether what they termed "fecundity" corresponds to what I have called "fecundity" or "productivity", although I suspect the former. In that case, one cannot be certain that a positive correlation between fecundity vs. food supply in that popuation was paralleled by a positive correlation between productivity vs. food supply. Fecundity equals productivity multiplied by cub sex ratio (Fc = C/L/IBI*%FC) and sex ratio may also be affected by food supply.

typical of many ungulates living at mid- to high-latitudes in the northern hemisphere. But whereas most of the ungulates breed just prior to implantation, the bears breed 3 to 6 months earlier. The delay of implantation may allow bears to postpone the "decision" as to whether body weight and condition are sufficient to support gestation and lactation until late autumn or early winter, despite the early breeding season (Rogers 1977).

6:III.C.2. Delayed Implantation: Another Perspective

Although one selection pressure possibly favoring implantation of embryos during autumn has been revealed by Rogers, the question remains of why breeding does not also occur during autumn. As a first step towards answering this question, 2 hypotheses are proposed:

1) Whereas nutrient-energy expenditures for finding and winning mates would be about the same at any time of spring, summer, or autumn, the amount of nutrient-energy income lost per unit time would be most severe when food supply is best. In most bear habitats, less food is available during spring and early summer--when breeding normally occurs--than in late summer and autumn when berries ripen and hard mast falls. (Tom Beck and Lynn Rogers independently derived the same hypothesis; pers. comm. 1984).

The early breeding season should be less adaptive in habitats where bears depend heavily on salmon, seals, ungulate neonates or carrion, or other foods which are particularly abundant during the breeding season. However, loss of nutrients and energy while searching for mates might be reduced at locations where rich foods are so concentrated that numerous bears aggregate to feed (e.g., on garbage in Yellowstone National Park, F. Craighead 1979; or on salmon at McNeil River on the Alaska Peninsula, Stonorov & Stokes 1972; Bledsoe 1975; Egbert & Luque 1975; Glenn et al. 1976).

2) Early onset of the breeding season, and the fact that it can be extended to at least 2 months, should allow virtually all estrus females time enough to encounter mates, even if the bears are widely dispersed. This hypothesis is substantiated by the fact that ovulation is also delayed until induced by copulation (Wimsatt 1963; Erickson 1964; J. Craighead et al. 1969; Lono 1970).

6:III.C.3. Effects by Age or Parity of Females on Responses by Their Whelping Rate to Variations in Food Supply

Data on black bears from Rogers (1977) and Eiler (1981) indicates that as females mature. they show a decrease in the tendency to skip reproduction during famines of moderate severity. This agrees with information on Yellowstone grizzlies and other bear populations that interbirth interval declines with increasing maternal age or parity (J. Craighead et al. 1976; Stringham, in prep.)--provided that the interval is not already at a minimum for primiparous mothers (see Alt 1982). The decrease of interbirth interval coincides with the increase of litter size, and thus of productivity (C/L/IBI), with increasing maternal age or parity--although these trends may be reversed during senescence (Stringham, in prep.). Two hypotheses are proposed as possible explanations.

1) Perhaps fully mature females are larger, with greater bodily stores of nutrients and energy, than adolescents.

That hypothesis is not alone adequate, as suggested by the fact that the growth curves indicate attainment of nearly maximum size several years before vulnerability to famines is minimized. However, more data on decline in skipping reproduction and in lengths of weaning-to-next-birth and interbirth intervals will be needed before this hypothesis can be tested more conclusively.

2) Decreasing vulnerability with increasing maturity may (also) be a function of experience or of higher dominance rank and control of resources that are either more abundant, more profitably harvested, or richer in critical nutrients--at least during periods when nutrient-energy balance is limiting.

6:III.C.4. Premature Estrus and Generation Length

As noted above at the end of Section B, some females begin copulating at least 1 year before they succeed in producing litters that survive long enough to be censused, if they conceive or implant at all (J. Craighead et al. 1969, 1974, 1982a; Jonkel & Cowan 1971; Rogers 1977; Eiler 1981). Two hypotheses have been proposed to explain that:

1) Rogers (1977, 1983) and Eiler (1981) suggested that nutrient-energy balance during the first estrus is sometimes too low for pregnancy or lactation to be maintained.

2) An alternate hypothesis, proposed by J. Craighead et al. (1974, 1982a) is that maturation of the induced ovulation mechanism sometimes lags behind that of other reproductive mechanisms; or copulation itself may be necessary for maturation of the induced ovulation mechanism.

Support for the former hypothesis is relatively strong, whereas I know of none for the latter hypothesis. Yet, evidence is too sparce for the latter to be dismissed.

Failure of a nulliparous female to reproduce even after she has had her first estrus and mated, will increase her puberty-to-first-whelping interval beyond the 0.5-year minimum. That will correspondingly increase generation length. So generation length should be negatively correlated with average food supply during maturation to puberty, and with supply during the puberty-to-first-whelping interval. If a female's first litter dies at such a young age, pre- or postnatally, that its existence is never detected, then generation length may seem even longer than it actually is.

6:III.D. Interbirth Interval vs. Maturation and Recruitment Rates

Comparisons among over 20 populations of grizzly, black, and polar bears reveals a positive (sigmoid) relationship between interbirth interval vs. generation length (Stringham, in prep). This is probably due at least partially to (1) the effects of maturation rate on (a) age at weaning [thus, on length of the birth-to-weaning portion of the interbirth interval, the BWI] and on (b) age at puberty, as well as to (2) the effects of food supply and nutrient-energy balance on maturation rate and on lengths of the intervals (a) between weaning of one litter and birth of the next [WNBI] and (b) between puberty and first whelping [PRWI]. (Fig. 6:1, p.157). Recall that:

IBI = BWI + WNBI and G = AP + PFWI

Whether interbirth interval is positively or negatively correlated with food supply may depend upon whether supply is measured at the beginning or end of the interval (e.g., at the birth-to-weaning interval vs. at the weaning-to-next-birth interval), or averaged over the entire interbirth interval. (Fig. 6:1, p.157).

1) If food supply and the mother's nutrient-energy balance are good when litters are produced, a higher proportion of the litters may survive until weaning. That would tend to produce a positive correlation between the birth-to-weaning interval vs. food supply and nutrient-energy balance at the beginning of the interval--i.e., circumnatally. So the same would tend to be true for the entire interbirth interval. (Fig. 6:1, p.157).

2) The relationship between the birth-to-weaning interval vs. food supply and nutrient-energy balance can also depend upon maturation rate, where faster-maturing litters are weaned at a younger

age than slower-maturing litters (see Strogonov 1969:132; Jonkel & Cowan 1971). (Fig. 6:1). The maturation-accelerating effects of high food supply and nutrient-energy balance would tend to shorten the birth-to-weaning interval and thus the entire interbirth interval, contrary to the effects of food supply and nutrient-energy balance of immatures on their own recruitment rates. Relative strengths of the contradictory impacts by maturation rate vs. recruitment rate on lengths of the birth-to-weaning and interbirth intervals have not yet been determined; they probably vary circumstantially.

3) If food supply and nutrient-energy balance are poor during the summer when surviving litters are weaned and the mother can breed again, she may not whelp during the following spring, lengthening her weaning-to-next-birth interval; or else the litter may be lost in spring before it can be censused. Respectively, these 2 scenarios either actually or apparently lengthen the interbirth interval associated with her previous litter. So there should tend to be a negative correlation between length of the weaning-to-next-birth interval vs. food supply and nutrient-energy balance during that interval (WNBI). Likewise, length of the entire interbirth interval should tend to be negatively correlated with food supply and nutrient-energy balance at the end of that interval (IBI) (Fig. 6:1).

4) In comparisons among populations, estimated interbirth intervals were negatively correlated with indices of food supply and nutrient-energy balance. This suggests that interbirth interval was governed by maturation rate to weaning more than by litter recruitment

rate. That interpretation is corroborated by the strong positive correlation between interbirth interval vs. generation length--i.e., vs. maturation rate to puberty or first whelping (see Stringham 1980, in prep). The data from most populations on interbirth intervals seems to be concentrated on females which reared their cub litters to weaning; indeed, some estimates of interbirth interval were based on mean age at weaning. Juvenile recruitment rates are not known for most of these populations.

5) By contrast, for YNP grizzlies, mean interbirth interval was positively correlated with indices of food supply and nutrient-energy balance at the beginning of each interval. This suggests that in YNP, interbirth interval was governed more by recruitment rate than by maturation rate of the litters. Although correlations between per capita recruitment rates vs. interbirth interval are non-significant and weaker than one might expect, that could be an artifact of knowing interbirth intervals for only about one-third of the censused litters. Furthermore, although data are not available specifically on recruitment rate for litters, recruitment rate for individual offspring to average weaning age (2.5 or 3.5 years) was positively correlated with food supply at the beginning of each interbirth interval, corroborating the above interpretation. Nevertheless, without data on maturation rates for those offspring, this hypothesis--that effects of maturation rate on the birth-to-weaning interval were dominated by those of recruitment rate--remains unconfirmed.

Because the end of each interbirth interval coincides with the beginning of the next, food supply during year t might tend to be negatively correlated with length of the interval just ending, but positively correlated with that just beginning.

Relative strengths of correlations between parameters of reproduction and recruitment vs. indices of food supply and nutrient-energy balance (or biosocial factors) depend not just on how sensitive each parameter is to that environmental (or biosocial) factor, but also on (1) how subject the parameter is to sampling bias and to (2) perturbation by intervening endogenous or exogenous influences: (1) The annual value for density of cub litters is obtained by summing all litters observed; it is based on a single cumulative sample. The same is true for cohort sizes at ages 0.5-2.5. By contrast, each litter censused is a single sample for litter size; so the annual mean for litter size each year is based on numerous samples, making it less sensitive to sampling error. Interbirth intervals are also based on numerous samples. Although the interval could potentially be documented for every litter whelped during each year, doing so is impractical; so interbirth interval tends to be less well sampled than litter size. (2) Although <u>mean</u> whelping rate should be approximately the inverse of the mean interbirth interval, "chance" events would tend to preclude equal proportions of the females whelping each year and to disrupt any tendency for regular cycling. Such "chance" events include irregularities in densities of adult females recruited each year minus the density lost to death, emigration, or sterility. Such "chance" events could thus endogenously induce "random" fluctuations in whelping level, interbirth interval, and most other parameters of reproduction and recruitment <u>except</u> cub litter size, even in lieu of impacts on those parameters by exogenous influences (e.g., FS-NEB). The fact that litter size is the parameter least subject both to sampling error and to endogenous random fluctuation, may explain why it shows the strongest correlations with the total food supply and nutrient-energy balance indices, and with certain biosocial factors, as shall be demonstrated in Chapter 8:II.A.

6:IV. CUB LITTER SIZE

Evidence of a positive correlation between cub litter size vs. food supply and nutrient-energy balance has been provided by several investigators. (1) As mentioned earlier, cub litter size in grizzly and polar bears is highest at low latitude or coastal habitats where adults tend to be largest in size and where food supply and climate tend to be most favorable (Stringham 1980, Chapter 5:I.B; Bunnell & Tait 1981). (2) For black bears in North America, litters tend to be larger in the East than in the West, in correspondence with differences in average adult body weights and presumably in food supply and nutrient-energy balance (Reynolds & Beecham 1980; Bunnell & Tait 1981; Section II.B., above). (3) When Beecham (1980a,b) compared between 2 black bear populations in Idaho, he found that litter sizes averaged larger in the population where the bears grew and matured faster--a difference he attributed to habitat quality, presumably in terms of food supply and nutrient-energy balance. (4) On the Upper Peninsula of Michigan, mean litter size for females seen at garbage dumps by Rogers et al. (1976) (3.1 C/L, n=7) was larger ($P:2t < 0.01$) than that seen in the same area, away from garbage sources (1.99 C/L, n=129) by Erickson et al. (1964). (No mention was made by Rogers et al. of how the supply of natural foods or climatic severity might have changed during the intervening years). Similar results were reported by Eiler (1981) for Smoky Mountains black bears.

One limitation on those findings from comparison among populations is that they are based on cub litter sizes several months postpartum. They do not reveal whether food supply and nutrient-energy balance affected cub litter size at censusing by affecting it prenatally and at birth, or only by affecting survival rate between birth and censusing. That question could be best answered by assessing the relationship between prenatal food supply and nutrient-energy balance of the dam vs. (a) prenatal or neonatal litter sizes and (b) postnatal survivorship. Unfortunately, data on prenatal and neonatal litter sizes is too sparce to serve as a basis for testing whether they are positively correlated with prenatal food supply or the dam's prenatal nutrient-energy balance. Nor can that question be answered with Rogers's 5 years of data on Minnesota black bears or with the 23 years of data on Yellowstone grizzlies, since litter sizes for these latter populations were evaluated several months postpartum.

A surprising feature of Roger's data is the stability in density of cubs despite major variations in food supply and in whelping rate and level (Fig. 6:2, p.160). There were 14 cubs per year during 1971-73 and 15 per year during 1974-75 on Rogers's study area Although this reveals cub density to have been relatively unaffected by variations in food supply, even this minor change in cub density was negatively correlated with prenatal food supply ($r = -0.667$). Because cub density (#C) was negatively correlated with prenatal food supply, cub litter size must have been even more negatively correlated with prenatal food supply (#C/#L = #C/L). Indeed, the coefficient I obtained is -0.805, based on my estimates for litter size in that population. Although Rogers did not provide data on annual cub litter size means, they can be estimated from the information he did provide on cub density and whelping level. His data for cub density during June is from residents on his primary study area; that for whelping level (cub litter density) and whelping rate is from both residents and some non-residents of that area. If whelping level among just residents was closely correlated with that for residents and non-residents combined, then whelping level for the larger group would provide an index of that for the smaller, enabling the reviewer to calculate an index for June litter size among the residents (see Table 3:4, p.32). The estimates for litter size will not be exact. However, to the extent that they are correlated with actual litter sizes, the estimates will serve as a basis to test for correlations between litter size vs. food supply and other controlling factors.

Results from such tests reveal a weak positive correlation between June litter size vs. postnatal food supply (Tables 6:3 and 6:4, pp. 161, 163); that might reflect effects of spring food supply and nutrient-energy balance on cub survivorship to June--a relationship which Rogers documented more thoroughly for particular families, as shall be detailed below in Section V:A. However, as noted above, those results also indicate a strong negative correlation between June litter size vs. prenatal food supply (r = -0.805). Again, let it be emphasized that this negative correlation is not likely to be an artifact of errors in estimating litter size, since total cub density was also negatively correlated with prenatal food supply. Rather, what needs explanation is the minor increase in cub density associated with a trend of major but transient increase in postnatal food supply and in whelping rate and level.

One might hypothesize that the negative correlations between prenatal food supply vs. cub density and litter size are artifacts of some intervening influence. Perhaps changes in average ages of adult females from year to year, and consequent age-dependent changes in mean litter size (see Stringham, in prep.), could have masked a positive effect or a non-effect of food supply and nutrient-energy balance on litter size. On the other hand, the negative correlation between cub density and litter size vs. food supply could be just an artifact of the small sample size. Had data on cub density and litter size been collected for as large a population over as many years as data on whelping rate and level (5 vs. 8 years), positive correlations might have also been found between cub density and litter size vs. food supply. It is a matter warranting further investigation.

In any case, Rogers (pers. comm.) has suggested that natal litter size is not affected by prenatal food supply and nutrient-energy balance of the dam--contrary to the usual pattern among mammals (see Stringham, in prep.). If not, that might be explained by the following hypothesis:

> It is typical among ungulates in temperate and boreal habitats of the northern hemisphere that ovulation, conception, and implantation occur during the breeding season, shortly before winter. Apparently, therefore, that is when their "decision" is made as to how much investment to make in reproduction--whether or not to ovulate at all, and of how many ova to shed, or how many blastocysts to implant.
>
> Even though sympatric bears make comparable decisions at about that same time of year, that is several months after their own breeding season. Because bears breed in the spring and early summer, long before pre-winter nutritional status has been established, they delay implantation until such an assessment can best be made--at the onset of hibernation (Rogers 1976).
>
> Because of the long time-lag beween ovulation and implantation, mothers may not be able to adjust their corpora luteal (ovulatory) or zygotic litter sizes to pre-hibernation nutritional status. Rather, they may initially be able to decide only whether or not to reproduce, all or none, and only later how

> much to invest per litter, and thus how large a litter to rear. Adjustment in litter size might have to be made postnatally. One way that this might be done is by hierarchial investment among cubs within the litter, perhaps on the basis of sex or by permitting competition and dominance among the cubs themselves (see Stringham, in prep; and Section VI, below).

At least preliminary testing of that hypothesis could be done by checking data on prenatal and natal litter sizes vs. prenatal food supply and nutrient-energy balance of the dam for other mammals exhibiting delayed implantation.

6:V. RECRUITMENT

6:V.A. Minnesota Black Bears

Even if natal litter size were positively correlated with prenatal food supply and nutrient-energy balance of the dam, parental investment per cub might be inversely related to litter size (see Stringham, in prep). That inverse relationship should be even clearer in the absence of a positive correlation or existence of a negative correlation (as may have occurred for Minnesota black bears) between natal litter size vs. prenatal food supply and nutrient-energy balance of the dam. Furthermore, recruitment rate per cub should tend to be be positively correlated with average parental investment per cub. So, recruitment rate per cub should tend to be inversely related to cub litter size. This prediction is consistent with Rogers' (1976) finding for Minnesota black bears of a negative correlation between cub litter size at age 2 months vs. subsequent recruitment rate.

Recruitment rate between ages of about 2 to 17 months was positively correlated with pre-, post-, and circumnatal levels of food supply and nutrient-energy balance of the dam and cubs. Specifically: If berries were scarce both pre- and postnatally, survivorship was 24% (n=30); if scarce only prenatally, 42% (n=44); if scarce only, postnatally 60% (n=32); and if abundant both pre- and postnatally, 94% (n=17). In view of those results, it is not clear why survivorship to yearling age was uncorrelated with prenatal food supply, according to my analysis of Roger's data (Table 6:3, p.161). His figures may be based on a more select or more inclusive sample than that used as the basis of my calculations. At age 2 months, weights of entire cub litters were positively correlated with maternal pre-denning weights ($r = 0.735$, $P{:}2t = 0.001$). Maternal body weight during denning presumably affected amount and quality of the milk that could be provided to cubs, and thus how rapidly they grew and developed in the den, during the first 2 to 3.5 months postpartum.

After emergence from the den, survivorship for the next year was positively correlated with neonatal weights and with prenatal food supply. However, those effects were gradually subordinated to effects of postnatal food supply and cub body weight, as dams began foraging anew and cubs supplemented nutrition obtained by suckling with that obtained by foraging for themselves. Autumn pre-denning body weights of cubs, at an age of about 9 months, averaged 40% heavier ($P{:}2t <$

0.0001) during years of abundant nuts and fruit than during those of famine. Survivorship between ages of about 2 to 14 months seemed equally dependent on pre- and postnatal food supplies. But over the next few months, between ages of about 14 to 17 or even 21 months, survivorship was clearly less strongly influenced by food supply during the prenatal summer and autumn (t-2) than by that during the postnatal (t-1) summer and autumn. Rogers (1983:198) reports that "Nearly all yearlings that weighed less than 10 kg in late March died within 4 months, as did 7 of 9 which weighed 10 to 13 kg. None of the 15 heavier yearlings died." Over 90% of mortality for cubs and yearlings was from natural causes, primarily starvation; some additional mortalities were attributable to starvation-induced debilitation of these immatures or to elevated cannibalism by adults during famines. (Fig. 6:2, p.160; Rogers 1976, 1977, 1983, in prep.).

6:IV.B. Yellowstone Grizzlies

For Yellowstone grizzlies too, there is at least a hint of a negative correlation between 0.5-year cub litter size vs. recruitment rate over the next 2 years (r = -0.231, P:1t = 0.26, n=10), despite the fact that litter size and recruitment rate are both positively correlated with food supply and nutrient-energy balance.

The information on Minnesota black bears sufficed to reveal effects of prenatal levels of food supply and nutrient-energy balance on recruitment rate to an age of about 9 months, and of pre- and postnatal levels on recruitment through about 21 months. But comparison with results on Yellowstone grizzlies is constrained because Rogers did not mention how strongly yearling survivorship was related to prenatal food supply and nutrient-energy balance of the dam, or how strongly survivorship past an age of about 21 months was affected by food supply and nutrient-energy balance pre-, post-, and circumnatally.

Data on Yellowstone grizzlies suggests that food supply and nutrient-energy balance both pre- and postnatally, that is circumnatally, continued to affect recruitment rate to at least age 5.5 years, and perhaps lifelong. Furthermore, the correlation between density of recruits in each cohort vs. circumnatal food supply and nutrient-energy balance got stronger, not weaker, as the cohorts matured from age 0.5 to 5.5 years. Whatever effect those circumnatal conditions had, they seem to have been magnified rather than attenuated with time--despite any intervening influences of conditions concurrent with attrition from each cohort. Indeed, recruitment rates between ages 1.5 to 5.5 years were more strongly correlated with food supply and nutrient-energy balance circumnatally than for that concurrent with attrition (Tables 5:3, p.103, and 6:3, p.161). The same is true for interbirth intervals.

To have had such a lasting impact on the cohorts, food supply and nutrient-energy balance (or some correlated factors) presumably influenced not only quantity, but also quality of members in each cohort, in such a way as to affect their long-term capacity to compete for space and resources and to survive. This hypothesized

Table 6:5. Causes of attrition of grizzly bears from Yellowstone National Park, 1959-70.*

	Year and Number of Documented Deaths													
Cause of Death	1959	1960	1961	1962	1963	1964	1965	1966	1967	1959-67	1968	1969	1970	1968-70
Hunting	4	12	8	5	6	4	7	4	27	77	3	5	4	12
Control														
1. Problem bears killed	4	9	5	5	2	2	2	6	6	41	5	10	20	35
2. Bears moved from Ecosystem to zoos	1	1	2	0	4	0	0	0	2	10				
Human-caused accidental deaths	3	1	1	1	1	1	2	1	0	11				
Bear-bear deaths (Combat or infanticide)**	0	0	0	1	0	1	0	0	0	2				
Disease or Age	0	0	0	0	0	0	1	0	0	1				
All other deaths (cause unknown)	0	1	5	3	2	4	3	2	8	28				
TOTAL KNOWN DEATHS	12	24	21	15	15	12	15	13	43	170	21	23	53	97

* After F. Craighead (1979: Table 1). Data for 1959-67 from F. Craighead (1979); data for 1969-70 from J. Craighead et al. (1974) and Meagher (1978; cited by Schullery 1980).

** Although only 2 bear-bear deaths were tabulated by F. Craighead (1979: Table 1), several other cases of infanticide were reported by J. & F. Craighead (1967) and by J. Craighead (p.245, in Herrero 1972a).

relationship between quality vs. attrition is analogous to the well-known pattern for machines. For example:

> If groups of several brands of off-road vehicles were driven in an endurance competition cross-country through rugged terrain, all might complete the first portion of the race, fewer the second portion, and so on, until only the best machines remained. The better the quality of a brand of machine, the lower its average rate of attrition.

The same may apply to cohorts. Indeed, Strogonov (1969:132) cites reports from Siberia that bears which are runts as cubs are still runts as adults. The persistence of circumnatal effects through adulthood in bears also resembles the pattern for other mammals discussed by Trivers & Willard (1973)--which might be related to what Geist (1978) termed "phenotypic quality."

These possibilities will have to be explored by future research--along with the null hypothesis that the trend is merely spurious.

6:V.C. Comparative Data on Other Mammals

Trivers & Willard (1973) reviewed evidence that the condition of an animal prior to the end of parental investment often persists through adulthood. Mammals which are runts as infants, and which do not subsequently encounter unusually good food conditions as juveniles, are likely to still be runts as adults. This is consistent with data that average body size and recruitment rate within mammalian litters tend to be inversely related to litter size (just as Rogers found for black bears), presumably because pre- and postnatal investment per offspring is inversely related to litter size, despite any positive correlation between nutrient-energy balance of the dam vs. litter size. A theoretical model developed by S. Ellner and myself suggests why this might be so (see Stringham, in prep).

6:VI. CUB SEX RATIO

Trivers & Willard (1973) extended those insights to predict a positive correlation between nutrient-energy balance (condition) of dams vs. sex ratio of their offspring. They argued that receipt of above-average parental investment benefits sons more than daughters among typical polygamous vertebrates; for in such taxa, relative body size and condition affect reproductive success or fitness of adult males more than that of females. For example, even relatively low-ranking females normally succeed in reproducing, whereas low-ranking males may not.

In personal communication to Mech (1975), those authors noted that this prediction did not take into account the fact that maternal condition can also affect natal size of her litters, which might reverse the prediction about mean investment per cub, and thus about cub sex ratio--an assertion which is critiqued by Stringham (in prep.). However, if natal litter size in bears is indeed unaffected by prenatal food supply and nutrient-energy balance of the dam, then the original prediction of a positive correlation with natal cub sex ratio should supposedly apply. That still assumes for bears, of course, that dependency of reproductive success and fitness on circumnatal food supply and maternal nutrient-energy balance is indeed greater for males than for females--an assumption which seems reasonable, but cannot be tested with available data.

In any event, for Minnesota black bears, cub sex ratio seems uncorrelated with food supply, according to Roger's own evaluation of his data and to the correlation coefficients which I calculated (Table 6:3). Although for Yellowstone grizzlies, there is only a weak, non-significant positive correlation between cub sex ratio vs. postnatal FS-NEB, that could be a sampling artifact.

Recall that during 1959-68, prior to dump closure, food supply and nutrient-energy balance in YNP were normally so high that cub sex ratio--like cub density, whelping level, and whelping rate--was nearly uncorrelated with food supply and nutrient-energy balance. Results suggest a least a weak positive correlation between cub sex ratio and density vs. postnatal food supply and nutrient-energy balance. But lack of data on food supply and nutrient-energy balance for 1969 prevents one from detecting any possible influence by prenatal impacts of dump closure. If, even after 1970, most variation in cub sex ratio and density was still due to variation in male cub density, then there would have been a positive correlation between cub sex ratio vs. TFS-NEB equivalent to that between cub density vs. TFS-NEB. This possibility should be explored in future research. The likelihood that cub sex ratio was (also) controlled by biosocial influences is discussed in Chapter 11:III.B.3.b.

According to Alt (1982) for Pennsylvania black bears, litter size tends to increase as dams mature--as seems typical in bear populations (Stringham, in prep). Since cub sex ratio was positively correlated with litter size in that population, cub sex ratio may have also increased as the dams matured. That would be consistent with a positive correlation between cub sex ratio vs. maternal nutrient-energy balance.

For Yellowstone grizzlies, there seems to have been a positive correlation between cub sex ratio vs. cub density ($r = 0.690$, $P{:}1t = 0.02$). But this does not seem to have held among Minnesota black bears; in fact, the reverse may have occurred ($r = -0.410$, $P{:}1t = 0.75$, $n=5$). But, again, with data from only 5 years for Minnesota black bears, sample size may be too small to give reliable correlations.

6:VII. RELATIVE SENSITIVITIES OF DIFFERENT REPRODUCTIVE PARAMETERS TO DEFICITS OF FOOD AND ENERGY

Recall that for Yellowstone grizzlies, 0.5-year litter size was positively linearly related to all indices for food supply and nutrient-energy balance (total supply, supply per bear, and supply per unit bear mass). That is, litter size was equally sensitive to a change in the level of food supply and nutrient-energy balance at any observed level--although sensitivity probably declines at levels substantially lower and higher than those observed during 1959-81. By contrast, even within the range of food supply and nutrient-energy balance levels observed then, sensitivities of whelping level (number of adult females whelping each year) and cub density were inversely related to the average level of food supply and nutrient-energy balance. The same was found for whelping rate among Smoky Mountains black bears (Chapter 5:II.B.2; Eiler 1981) and among reindeer (Reimers 1983). In other words, when food supply and nutrient-energy balance were low, (a) mean litter size for females which succeeded in whelping and in rearing litters to at least age 0.5 year, was affected much less than (b) the number and proportion of adult females that succeeded. By contrast, even when food supply and nutrient-energy balance were so high that most females succeeded in whelping and in rearing at least 1 cub to age 0.5 year, litter size at that age size was still affected by variations in food supply and nutrient-energy balance.

For Canadian polar bears, Stirling et al. (1976) likewise reported that a serious decline in food supply and nutrient-energy balance affected litter size much less than it affected (a) proporation of adult females found with litters, and (b) abundance of offspring found with them. (In this case, offspring included not just cubs, but also older unweaned juveniles). This difference in sensitivities between litter size vs. whelping rate to food supply or nutrient-energy balance, might be explicable by a rephrased version the hypothesis formulated by Stirling et al. (1976) for polar bears. That new version is:

> Mothers which foraged most effectively or which were highest-ranking in direct "contest" competition for food (e.g., prey, carrion, or garbage) suffered little from food shortages, even during famine. They had little reduction in either conception rate or in pre- and postnatal cub recruitment. This showed up as a minor decline in mean litter size. However, for most females, nutrient-energy balance declined so badly during famine and severe weather that they either failed to become pregnant, or else lost their entire litters, either prenatally, or prior to censusing postnatally.

It was noted in Chapter 5 that interbirth interval and generation length for the McNeil River bears were longer than those for the other coastal populations at similar latitudes; in fact, they were comparable to what the regressions predict for inland populations at that latitude. This caused correspondingly low values for productivity (C/L/IBI) and reproductive vigor for McNeil bears, although cub litter size is comparable to that for the other 2 coastal populations. Apparently, rates of maturation to weaning and to puberty were retarded in the McNeil population. The proximity of McNeil River to heavily glaciated mountains or other factors might reduce the climate-ameliorating effects of its proximity to the ocean, compared to effects at Kodiak Island and Chignik-Black Lakes. But it is not apparent why that would affect maturation rate more than litter size. Granted, when food supply and nutrient-energy balance are low, maturation rate may be more sensitive than litter size. But the high litter size suggests that food supply and nutrient-energy balance were too high for that to be the factor determining the greater sensitivity by maturation rate in this case. On the other hand, slower maturation at McNeil was predicted by Stokes (1970)--years before that rate had been documented--on the basis of the high level of social strife at McNeil Falls, arising from the unusually high concentration of bears which aggregate there to feed on salmon. As many as 40 bears have been observed there simultaneously (see Stonorov & Stokes 1972; Egbert & Luque 1975; Bledsoe 1975). Only the aggregations of grizzlies at the Yellowstone dumps are known to have been higher. However, we cannot not yet exclude the possibility that cub litter size can also be reduced by strife, if not through a physiological stress response, then certainly by direct aggression against cubs. This point will be considered more fully in Chapter 9:IV.D.

6:VIII. EFFECTS OF DUMP CLOSURE ON BODY WEIGHTS OF YELLOWSTONE GRIZZLIES

Recall (Table 4:5, p.87, Chapter 5:II.C.) that the body weight data of Knight et al. (1981) and of J. Craighead & Mitchell (1982) were not presented in sufficient detail for a reviewer to calculate significance levels for the pre- vs. post-closure differences in weights for each age-class. So the differences can be considered only without assessment of their statistically reliability.

Although mean body weights of adult YNP grizzlies apparently declined after closure of the garbage dumps, the reverse was true for yearlings and 2-year-olds; mean weights of cubs seemed unaffected. This increase is body weights for 1- and 2-year-olds could be a side-effect of the decline in mean cub litter size. Irregardless of whether the decline in 0.5 year cub litter size was the result of (a) decline in natal litter size and/or in (b) survival rate between birth and censusing, the decline in cub litter size would have (pre- or postnatally, respectively) lowered the number of offspring competing for maternal investment. This might well have had more impact on weights of yearlings and 2-year-olds than on weights of cubs, since attrition from each litter would have been progressive. So, despite the presumed decline in total investment per surviving litter, the amount per cub could have actually increased, causing a comparable increase in body weights of juveniles. However, this would be reversed after weaning, when the offspring had to forage for themselves without access to abundant garbage.

6:IX. INTERVENING EFFECTS OF MAN-CAUSED ATTRITION ON RATES OF REPRODUCTION AND RECRUITMENT FOR YELLOWSTONE GRIZZLIES

Closure of the Yellowstone dumps certainly caused a drastic reduction in availability of manmade foods to the grizzlies and thus presumably in habitat carrying capacity. However, one must question how the influence of that on reproduction and recruitment was altered by concurrent changes in level of direct man-caused attrition. As availability of garbage at dumps declined, numerous grizzlies sought alternate sources of manmade foods, for instance garbage and groceries in campgrounds. In order to protect people and property, some of those grizzlies were removed by National Park Service personnel (Tables 3:3, p.31, and 6:5, p.183). According to Meagher (1978), during the 10-year period 1959-68, 28 grizzlies were removed from YNP by control actions, a level of 2.8/year; by contrast, during 1969-70, this level rose to 3.5-fold to 9.8/year. F. Craighead (1979; Table 6:5, p.183) gave higher figures for control actions of 5.6/year during 1959-70 vs. 15.0/year during 1969-70, a 2.7-fold increase. Documented control action losses remained high during 1971 (6) and 1972 (9), then dropped to about 1/year through 1978 (Meagher 1978; Schullery 1980). During 1959-66, documented loss of Yellowstone grizzlies to hunters averaged about 6/year; this rose to 27 during 1967, then fell back down to 4/year during 1968-70. Thus, the combination of increased levels of hunter kills and control actions during 1967-72 seems to have been largely responsible for the doubling in documented mortalities of Yellowstone grizzlies from 16/year during 1959-66 to 33/year during 1967-73 (J. Craighead et al. 1974; Table 3:3, p.31).

It is not clear how that increase in levels of hunter kills and control actions affected population density, dynamics, and infrastructure, of Yellowstone grizzlies. The population density figures given by J. Craighead et al. (1974; see Table 3:6, p.34) indicate a marked decline in total density for 1967, the same year that documented hunting pressure increased so drastically, albeit briefly. Despite the increased level of control actions, the census figures show increases in total density for 1968 and 1969, at a growth rate comparable to what the population had shown for 1962-66. Then density fell again for 1970. (Total density estimates available for 1971-81 were made in ways too different from those for 1959-70 to be compared here).

During 1968-70, density of adult females was nearly constant and density of adult males rose slightly, despite the almost 4-fold increase in levels of documented mortality for them: 5.1 adults/year during 1959-67 vs. 19.0 adults/year during 1968-72 (Tables 3:3 and 3:6, pp.31, 34). Some of this capacity to maintain or increase density of adults despite an increase in documented mortalities for them could have been due to a number of factors, including: (1) a coincidentally high rate of recruitment from subadult ranks due to good food supply and other favorable conditions several years earlier when these adults were conceived and born. (2) Some may also have been due to increased immigration from peripheral areas of the Yellowstone ecosystem (Chapter 12:I.A.3). If so, then the pool of potential immigrant subadult and adult females may have been declining despite stability in density of resident females, in which case the overall effect of control actions on subadult and adult female density would have gone unnoticed, at least temporarily. (c) There may have been some decline in mortality due to other causes. Finally, (d) the increase in number of documented mortalities may have exaggerated the increase in mortality level, due to more thorough documentation of mortalities during the latter period.

But whatever the means by which density of resident adult females was maintained, despite increased level of documented attrition for them, their stable density would seem to lessen the possibility that any of the decline in whelping level or rate associated with dump closure was due to the apparent increase in level of attrition for adult females. Likewise, since documented attrition due to control actions and hunting dropped back down to a low level after 1972, it seems unlikely to have caused a decline in adult female density then sufficient to account for the concurrent low levels for densities of cub litters and of cubs.

6:X. AUTOCORRELATIVE BIASES

Although there might be some autocorrelative bias in regressions of cub density and sex ratio vs. food supply per bear or per unit bear mass, such bias is probably neligible, as explained below.

Any regression of cub density vs. current (postnatal) food supply per bear, or per unit bear-mass,

$\#C_t$ vs. $[FS/N]_t$

$\#C_t$ vs. $[FS/BM]_t$

involves an element of autocorrelation. For cubs during year t are encompassed in the figure for total population size during that <u>same</u> year, i.e.,

$$N_t = \#C_t + (\#\text{ other grizzlies})_t.$$

In other words,

$$\#C_t \text{ vs. } [FS/(N)]_t$$

$$= \#C_t \text{ vs. } [FS/(\#C + \#\text{other grizzlies})]_t$$

Even where there is no inherent negative correlation, that autocorrelation would tend to introduce some--since cubs are in the numerator on one side of the equation and in the denominator on the other side (Chapter 9:I.C). So the positive correlations found between

$$\#C \text{ vs. } [FS/(N)]_{\text{postnatal}} \quad \text{and}$$

$$\#C \text{ vs. } [FS/(BM)]_{\text{postnatal}}$$

are probably weaker than they should be. But any such error is probably small since cubs are only a fraction of the total population and an even smaller fraction of the total biomass.

The problem of autocorrelation arises again in a slightly different way in regressions of cub sex ratio vs. FS/N and FS/BM, since sex ratio is the proportion of cubs that were male

$$\#MC/\#C \text{ vs. } [FS/(N)]_{\text{postnatal}} \quad \text{and}$$

$$\#MC/\#C \text{ vs. } [FS/(BM)]_{\text{postnatal}}$$

In this particular case, autocorrelation is further weakened by the fact that sex ratios were determined for only about 20% of the cubs. Additionally, autocorrelative bias can not a problem when one regresses cub density or sex ratio each summer vs. food supply per bear or per unit bear mass during the previous year, i.e., prenatally.

$$(\#C)_{t+1} \text{ vs. } [FS/N]_t \text{ or vs. } [FS/BM]_t$$

For N_t does not encompass $\#C_{t+1}$.

Recall that for 1959-81, correlations between cub density vs. prenatal levels of FS/N and FS/BM give results similar to those for postnatal levels. So any distortion by autocorrelation was apparently negligible. The same probably also applies in the case of cub sex ratio--an hypothesis which cannot be adequately tested due to lack of cub sex ratio data past 1970.

6:XI. COMPARISON AMONG INDICES FOR FOOD SUPPLY AND NUTRIENT-ENERGY BALANCE FOR YNP GRIZZLIES

Thus far, results for Yellowstone grizzlies have been discussed jointly in terms of all 3 indices of food supply and nutrient-energy balance for YNP, except when referring to the 1971-81 period when data was available only for total food supply (TFS-NEB), and not for supply per bear (TFS/N-NEB), or per unit bear mass (TFS/BM-NEB). Now let us compare results among those 3 indices during 1959-70 when all could be calculated. Although none of the 3 indices is markedly superior for all of the parameters of reproduction and recruitment considered, on average, supply per bear was a better predictor than total supply (P:1t = 0.01), and supply per unit bear mass was better yet (P:1t < 0.0001). (Paired t-tests were used to evaluate significance of those differences. Unpaired t-tests gave similar results.)

r: TFS-NEB < TFS/N-NEB < TFS/BM-NEB

Indeed, that is exactly the pattern one would expect. All other factors being constant (AOFBC), individual nutrient-energy balance should be more closely dependent upon supply per unit bear-mass than upon (a) mean supply per bear, irrespective of body mass or size, and than is (b) total supply of food available to the population, irrespective of population size and how that food is subdivided among the bears. Furthermore, deduction suggests that the amounts of nutrients and energy available for investment in offspring would depend not on the absolute average amounts consumed, but on the amounts consumed in excess of expenditures for maintenance and growth.

When one takes into account not only the amount of food available to the grizzlies, but also the potential share per bear or per unit bear mass, one begins to integrate the influences of climate and food supply with the influences of density and biomass. Chapters 7 to 9 analyze and discuss the relationships between reproduction and recruitment parameters vs. various biosocial influences, particularly population density and biomass, as well as density and behavior of adult females and males, and adult sex ratio. Chapters 10-12 give a general discussion of results, encompassing both environmental and biosocial factors. They interpret results in terms of (a) possible spurious indications of density dependence (Chapter 10), (b) social behavior (Chapter 11), and (c) the applicability of results on Yellowstone grizzlies to other bear population (Chapter 12). Chapter 13 integrates basic concepts for density independent and dependent influences with those for adult sex ratio and food supply into a complex stock-recruitment model from which a population model will be developed.

6:XII. SUMMARY

1) Climate can affect gross status of entire ecosystems and of some species within them. So climatic indices are potentially useful for explaining and predicting dynamics of individual populations.

2) The utility of Picton's climatic index is evident from its capacity for predicting rates of reproduction and recruitment for grizzlies, deer, and wapiti. However, we have yet to understand how the October-May means for temperature and precipitation actually affected natural food supply and nutrient-energy balance of the bears.

3) Furthermore, magnitude of climatic shifts largely determines the degree to which those shifts dominate effects by other factors on ecosystems or individual species.

4) There are clear indications of a positive correlation between summertime cub litter size vs. food supply and nutrient-energy balance indices in black bears (Hatler 1967; Jonkel & Cowan 1971; Rogers 1976, 1977; Beecham 1980a,b; Eiler 1981) and polar bears (Bunnell & Tait 1981). That was also documented here for grizzly bears by comparing among populations on the basis of latitude and habitat type, and among years for the Yellowstone population.

However, it is unclear whether food supply and nutrient-energy balance affect litter size at conception, implantation, or birth, or only via postnatal mortality. Theoretical considerations in terms of physiological ecology suggest that only postnatal mortality should relate litter size to food supply. But there is no data on prenatal or natal litter sizes with which to test this hypothesis.

5) The theory of Trivers & Willard (1973) predicts a positive correlation between cub sex ratio vs. maternal condition. Only weak evidence of a positive correlation between cub sex ratio vs. indices of food supply and nutrient-energy balance was found for Yellowstone grizzlies. But that weakness might be an artifact of having sex ratio data only when the level of food supply and nutrient-energy balance was high. Evidence of a positive correlation between cub sex ratio vs. nutrient-energy balance can be tentatively inferred for Pennsylvania black bears, but none was found vs. food supply for Minnesota black bears (Rogers, pers. comm.; personal calculations with Roger's 1977 data).

6) Positive correlations between maturation rate vs. food supply and nutrient-energy balance are evidenced by: (a) Positive correlations between rates of maturation vs. growth in black bears (Rausch 1961; Rogers 1976, 1977; Beecham 1980a,b; see also Jonkel & Cowan 1971 and Eiler 1981). (b) Positive correlations between interbirth interval and generation length vs. latitude for grizzlies (Chapter 5:I.A). (c) That is substantiated by the negative correlation between adult body weights vs. latitude.

7) The tendency for negative correlations between adult body size vs. latitude, induced by the relationship between nutrient-energy balance vs. latitude, may be somewhat counteracted by the advantages

in cold climates of large body size for reducing surface-to-volume ratio.

8) Positive correlations between whelping rate or level vs. food supply and nutrient-energy balance are evidenced by results of: (a) Comparing proportions of adult female black bears with cub litters in spring or summer vs. food supply during the previous summer and autumn (Jonkel & Cowan 1971; Rogers 1976, 1977; Eiler 1981). (b) Comparing density of cub litters each summer vs. indices for food supply and nutrient-energy balance pre-, post-, and circumnatally for Yellowstone grizzlies. In cases where litters were not censused until age 0.5, this could conceivably represent effects of food supply and nutrient-energy balance on postnatal litter survival, rather than on rates of litter conception, implantation, and whelping.

9) For Yellowstone grizzlies, interbirth interval was positively correlated with postnatal food supply and nutrient-energy balance. This is thought to be due to the effects of FS-NEB on litter survival rate and the truncation of interbirth intervals for litters that do not survive until weaning. However, interbirth interval data is available on only 36% of the litters censused, litters whose survival rates aren't known. So this hypothesis cannot be tested directly. But some support is found in (a) the weak positive correlation between interbirth interval for that 36% of the litters vs. mean recruitment rate for all cubs in each cohort, and in (b) the fact that both interbirth interval and recruitment rates are positively correlated with food supply and nutrient-energy balance.

10) For Minnesota black bears, Rogers (1976, 1977, in press, in prep.) documented positive correlations between pre- and postnatal food supplies vs. body weights to at least age 21 months. For Yellowstone grizzlies, there is a positive correlation between circumnatal food supply vs. recruitment rate to at least age 5.5 years. The circumnatal effects of FS-NEB on attrition seem to have dominated those of FS-NEB concurrent with the attrition. Apparently, conditions during gestation and infancy affect cohorts--perhaps in terms of their phenotypic quality--in ways which persist into adulthood. This is consistent with data on other mammals cited by Trivers & Willard (1973) and may be related to characteristics of "phenotypic quality" observed by Geist (1978) in wild sheep (*Ovis* spp.).

11) Rogers (1976, 1977) hypothesized that the delay of embryo implantation until autumn, near the onset of hibernation, allows bears to "decide" whether or not to implant on the basis of the dam's nutrient-energy balance--her capacity to produce and rear the litter.

But that would not explain why breeding does not also occur in autumn. One hypothesis is that breeding occurs earlier in the year because that is when there tends to be least loss of nutrient-energy income due to reduced foraging while trying to mate.

12) Evidence on Canadian polar bears (Stirling et al. 1976), Smoky Mountains black bears (Eiler 1981), and Yellowstone grizzlies, indicates that sensitivity to fluctuations in food supply and nutrient energy balance is inversely related to the mean level of FS-NEB in the

case of whelping rate, densities of cub litters, cubs, and older immatures, as well as in rates of recruitment/attrition. By contrast, sensitivity of cub litter size seems much more uniform over a wide range of levels in FS-NEB--although mean litter size cannot fall below 1 C/L and probably does not exceed 3 or 4 C/L for grizzly and polar bears or 5 C/L for black bears.

13) Closure of the YNP garbage dumps and the coincidental worsening in climate were accompanied by declines in various parameters of reproduction and recruitment. Body weights of adults also declined; but those of immatures of ages 0.5-2.5 did not. In fact, weights of 1.5- and 2.5-year-olds seem to have increased. That might be due to an increase in parental investment per surviving offspring caused by a smaller litter size at birth or at least by age 0.5 year.

14) Dump closure was also associated with an increase in level of attrition for subadults and adults. This was due at least partially to increased levels of hunter kills during 1967 and of control actions during the next few years. Although this might have reduced the density of adult females in the entire Yellowstone Ecosystem, it apparently did not reduce their density within the area where observations by the Craighead research team were focused. If that was also true after 1970, then the decline in litter density (whelping level) in YNP following dump closure would have reflected primarily a decline in whelping rate--as would be expected from the decline in food supply and nutrient-energy balance.

15) Three indices were used to evaluate relationships between food supply and nutrient-energy balance vs. parameters of reproduction and recruitment for Yellowstone grizzlies. Those indices are (a) total food supply--calculated by combining indices for natural food supply and nutrient-energy balance (climate) with that for garbage supply; (b) supply per bear; and (c) supply per unit bear mass. The former should be the best index for total food supply and the latter for nutrient-energy balance. Supply per unit bear mass was the most strongly correlated with most parameters of reproduction and recruitment, which presumably reflects the dependence of reproduction and survival on individual nutrient-energy balance more than on total food supply potentially available to the population. Food supply per unit bear mass and individual nutrient-energy balance reflect not only total food supply potentially available to the population, but also number of bears competing for it and the relationship between competitive ability and nutrient-energy needs relative to body size/weight/mass. That is, it encompasses some facets of density-dependence--the topic to which we shall now turn, within the larger context of biosocial influences on population dynamics.

PART III: RESPONSES TO BIOSOCIAL FACTORS

CHAPTER 7

COMPARISON AMONG GRIZZLY POPULATIONS

7:I. INTRODUCTION

For Yellowstone grizzlies or any other *single population*, responses by population dynamics to density or biomass can potentially be evaluated on the basis of either absolute number of bears censused or number per unit area of habitat (Chapter 8). These measures differ only in scale so long as area is constant, and not even in scale if the entire study area is designated as being of unit size. However, neither of those approaches will suffice for trying to relate differences in reproductive parameters *among populations* to corresponding differences in density or biomass.

Since absolute number of bears censused varies according to size of the area sampled, one would not expect *per capita* rates of reproduction and recruitment to differ among populations according to the absolute number censused (e.g., #C/L vs. #AdF). However, one might expect reproduction and recruitment to differ according to number of bears per unit area (e.g., #C/L vs. #AdF/ha). Indeed, as was shown in Chapter 5:I.A, maturation rate, cub litter size (C/L), productivity (C/L/IBI), and the reproductive vigor index, were all *positively* correlated with population density. However, that apparently reflects not any effect of density on reproduction and recruitment, but just the reverse. Population density seems to be directly dependent upon (positively correlated with) rates of reproduction and recruitment, which are in turn directly dependent upon nutrient-energy balance, which varies as a function of latitude and habitat-type (inland vs. coastal).

To detect density dependent relationships (negative correlations) between parameters of reproduction and recruitment vs. total population density, one would have to be able to quantify density not according to number of bears per unit area, but rather according to number per unit resource (e.g., food supply per bear or per unit bear mass). Unfortunately, no information is available on how food resources or nutrient-energy costs of living differ among populations--aside from what clues might be inferred from data on density itself or on latitude and habitat type.

Given then that absolute number (N) and number per unit area (N/A) are not equivalent when area differs substantially among populations, one cannot meaningfully compare among populations by regressing density of one age-class vs. density of another (e.g., #C/A vs. #AdF/A). For one thing, the latter regression involves an autocorrelation of form Y/Z vs. X/Z (see Chapter 9:I.C.1.b). Areas (A) occupied by the populations ranged over 4 orders of magnitude (2.61 - 13,625 km^2). Area studied has a far higher coefficient of variation than number of bears studied, either in total or in any specific age-sex class. Consequently, the +1.000 correlation between 1/A vs. 1/A dominates the relationship between the relative densities of different age-sex classes (e.g. for #C/A vs. #AdF/A, r = +0.9999), obscuring the relationship between relative numbers of bears in the different classes (e.g., #C vs. #AdF), which range over less than 2 orders of magnitude.

An alternative approach is to compare among populations strictly on the basis of infrastructure. For example, comparison among grizzly populations can be conducted in terms of relative numbers of adult males and females and of immatures in each population. This is done according to number of bears in the age-sex class relative to either (a) total population size (e.g., #C/N) or (b) density of adult females (e.g., #C/AdF). Hence, one can meaningfully regress other reproductive parameters (maturation rate, cub litter size, productivity, reproductive vigor, and density of cubs) against densities of specific age-sex classes (e.g., #C/L vs. #AdF/N). Even where this involves some autocorrelation (e.g., #C/AdF vs. #AdF or #C/N vs. #AdF/N), ranges of variation for population size and adult female abundance are similar enough to the ranges for abundances of other age-sex classes, not to obscure the biological relationships. (See Section III:A, below).

7:II. RESULTS

7:II.A. Infrastructure

7:II.A.1. Reproduction

7:II.A.1.a. Percents of Adults and Adult Sex Ratio

Comparison among 8 grizzly populations (Table 7:1) reveals that those with highest proportions of adults, relative to immatures, tend to have the slowest rates of maturation to weaning and first

Table 7:1. Reproductive and infrastructural parameters correlated to proportions of adults in 8 grizzly populations.*

	Adults			
Parameter	%F&M	%Females	%Males	M/F
Interbirth interval (IBI)	0.716 0.02	0.353 0.20	0.815 0.007	0.791 0.01
Generation length (G)	0.714 0.02	0.407 0.16	0.781 0.01	0.690 0.03
Cub litter size (C/L)	-0.548 0.08	-0.167 0.35	-0.684 0.03	-0.766 0.01
Productivity (C/L/IBI)	-0.689 0.03	-0.307 0.23	-0.804 0.008	-0.820 0.006
Reproductive vigor index (RVI)	-0.723 0.02	-0.361 0.19	-0.820 0.006	-0.794 0.009
Percent cubs (#C/N)	-0.689 0.04	-0.113 0.41	-0.871 0.005	-0.943 0.001
Cubs per adult female (C/AdF)	-0.864 0.006	-0.463 0.15	-0.904 0.003	-0.817 0.01
Percent yearlings (#Y/N)	-0.854 0.007	-0.850 0.008	-0.664 0.05	-0.331 0.23
Yearlings per adult female (Y/AdF)	-0.788 0.02	-0.889 0.004	-0.552 0.10	-0.189 0.34
Percent subadults (#SAd/N)	-0.737 0.03	-0.838 0.009	-0.513 0.12	-0.085 0.43
Subadults per adult female (SAd/AdF)	-0.730 0.03	-0.958 0.0004	-0.433 0.17	-0.034 0.53
Combined P:1t for G & C/L	0.002	0.056	0.0002	0.0003
Combined P:1t for G, C/L, & %C	<0.0001	0.02	<0.0001	<0.0001

Data from Tables 3:1 and 3:5; see Fig. 7:1.

whelping, judging from correlations with interbirth interval and generation length (Fig. 7:1). They also tend to have the smallest cub litter sizes (Fig. 7:1). Thus, they tend to have the lowest productivities, reproductive vigors, and proportions of cubs. (Recall that reproductive vigor is an index for the net impact of reproductive rate on population growth rate). This pattern of correlations for reproductive parameters (RPs) vs. percent total adults also holds strongly for (a) percent adult males and for (b) the ratio of adult males per adult female, but (c) only weakly for percent adult females (Table 7:1)

r: |RPs vs. #Ad/N, #AdM/N, #AdM/AdF| > |PRs vs. #AdF/N|

That is consistent with the earlier findings on just 6 of these populations by Stringham (1980).

Similarly, ratios of cubs, yearlings, and subadults per adult female were negatively correlated with the ratio of adult males per adult female and with percents of adult males, females, and total adults in the population. There are stronger negative correlations between the ratio of cubs per adult female vs. (a) the ratio of adult males per adult female and vs. (b) percent adult males, than vs. (c) percent adult females.[1]

r: |#C/AdF vs. #AdM/AdF, #AdM/N| > |#C/AdF vs. #AdF/N|

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[1] Results for adult sex ratio calculated as #AdM/Ad were similar to those for #AdM/AdF. The former way of presenting sex ratio data was used in discussion of the individual populations and would have been used here too, were it not redundant with results for #AdM/AdF. The latter ratio had to be used here as a basis of comparison with ratios of cubs and older immatures per adult female.

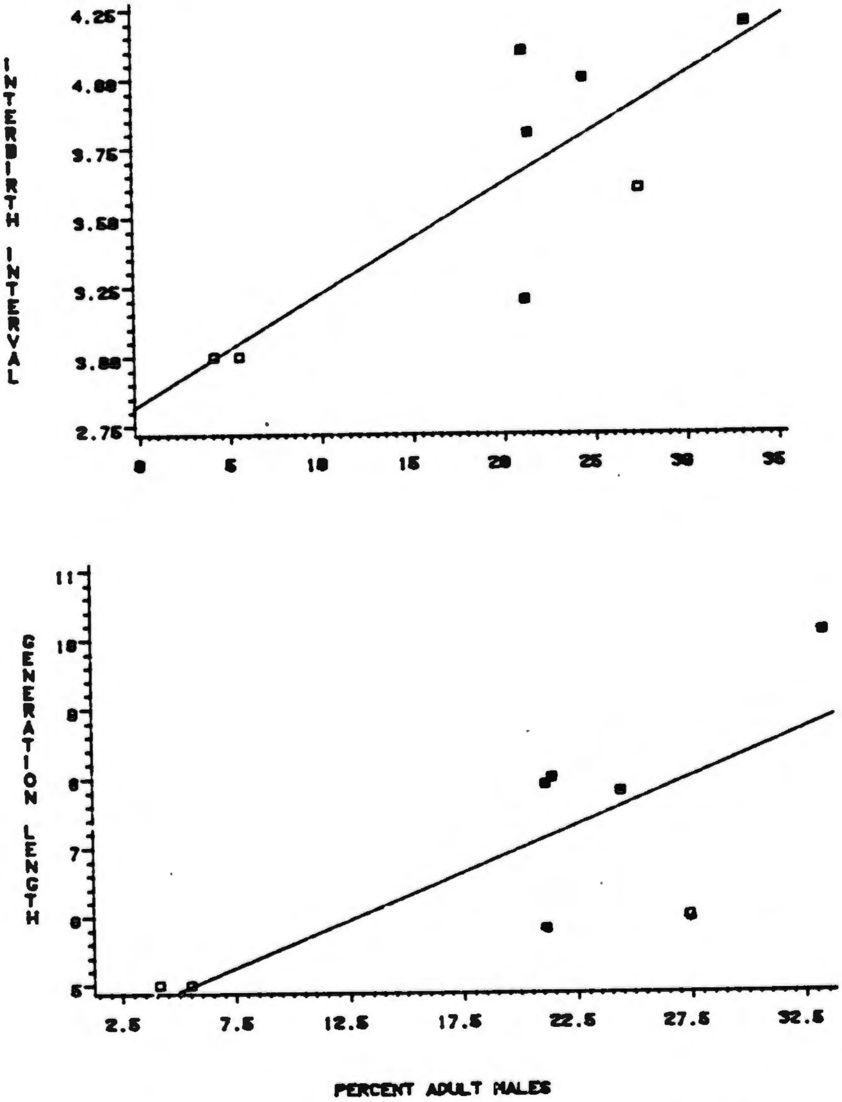

Fig. 7:1. Reproductive parameters regressed on adult male abundance (%) in each of 7 North American grizzly populations. (■ inland, □ coastal). (Data from Tables 3:1 and 3:5; see Table 7:1 for r and P).

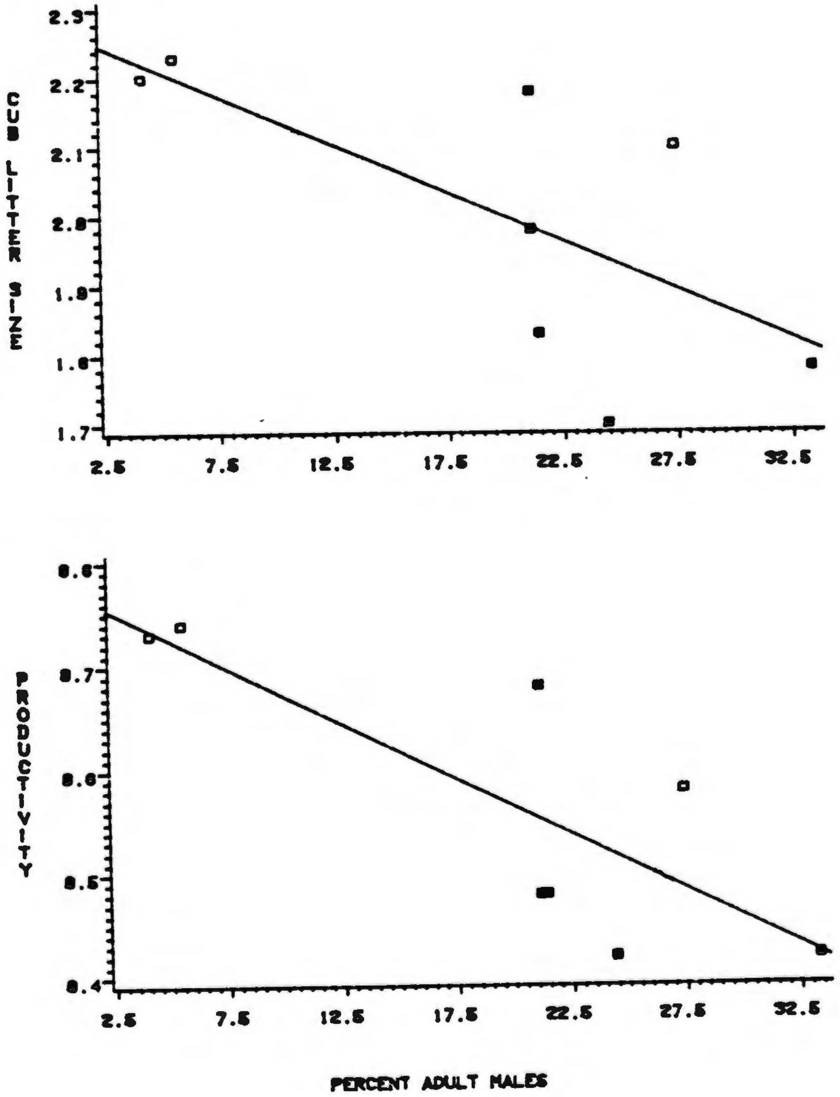

Fig. 7:1. (Continued)

Even though significance levels for correlations between reproductive parameters vs. percent adult females are too high--confidence levels too low--to be reliable individually, they are considered reliable in combination. That is for 2 reasons: (1) All parameters of reproduction are negatively correlated with percents of both male and female adults. (2) Combined significance levels are relatively low, even for females, as explained below.

The combined significance level for 2 or more mutually <u>independent</u> parameters is estimated by multiplying their individual significance levels. Here, the only reproductive parameters one can be reasonably sure are mutually independent are maturation rate (as indicated, for instance, by generation length), litter size, and perhaps percent cubs. The 1-tailed significance levels for their individual correlations with percent adult females are, respectively, 0.35, 0.16, and 0.41. The corresponding combined significance level for correlations with all 3 parameters is 0.02. This and other combined significance levels for these parameters are given at the bottom of Table 7:1. If some of the other reproductive parameters are independent enough to also be encompassed in calculations of combined significance level, then the actual combined level would be even lower--confidence level higher--than these values indicate.

The fact that reproductive parameters (RPs) are correlated with (a) percent adult males and (b) the ratio of adult males per adult female, more strongly than with (c) percent adult females,

r: |RPs vs. #AdM/N, #AdM/AdF| > |RPs vs. #AdF/N|

can be explained by 3 properties: (1) Percent adult females was less variable among populations than percent adult males--just as occurred within the Yellowstone grizzly and Minnesota black bear populations--and thus could have exerted less impact, even if per capita impact by adult females were as high as that by adult males. Means and standard deviations for percents of adult males and females were, respectively, 19.8% ± 10.1% vs. 26.6% ± 5.9%. Indeed, most variation in adult sex ratio (#AdM/Ad) was due to variation in relative abundance of adult males; percents of adult males and females respectively *statistically* account for 82% and 5% of variance in adult sex ratio (*causally*, they account for 100%). (2) Adult males may have a greater per capita density dependent impact than adult females, in accordance with their larger body size and higher dominance rank. This is indicated by analysis of demographic data for Yellowstone grizzlies (Chapter 8), and by observations of aggression by adult males against adult females and immatures, particularly in the Yellowstone and McNeil populations (Hornocker 1962; Stokes 1970; Stonorov & Stokes 1972; Egbert & Luque 1975; Bledsoe 1975; Chapter 11:II). (3) By contrast, adult females should have greater per capita "density independent" impact on reproduction. So long as there are enough adult males to impregnate all fertile adult females, adding additional adult males should not enhance reproductive rate, but just the opposite. Yet adding additional adult females might increase overall productivity for the population, even if it decreases per capita productivity. Because of the stronger density independent effects and weaker density dependent effects by adult females, relative to adult males, reproductive parameters are likely to be less negatively correlated with density of adult females than with density of adult males.

7:I.A.1.b.. Percents of Immatures

Reproductive parameters are strongly positively correlated with percent cubs, less strongly correlated with percent yearlings, and negligibly correlated with percent subadults (Table 7:2). Thus, there is a steady transition from the positive correlation between (a) other reproductive parameters vs. percent cubs (b) to the negative correlation between those reproductive parameters vs. percent adults. Apparently, as offspring mature, their relative abundance is increasingly affected by the factors which produce negative correlations between reproductive rate vs. percent adults, especially percent adult males--quite aside from any artifacts arising when comparisons are based on percentages of different age-classes within the same populations (see Section III.A.2).

7:II.A.2.. Survivorship and Recruitment

Difference in sizes of cub vs. yearling litters has been used by numerous investigators as an index for cub survivorship (e.g., Glenn et al. 1976). Figures on loss of cubs from known litters are available only from YNP (27%; F. Craighead & J. Craighead 1970) and McNeil River Game Sanctuary (38%: Glenn et al. 1976). Both are

Table 7:2. Reproduction and recruitment correlated to the proportions of immatures in 7 grizzly populations.*

Parameter	Age-Class Cubs	 Yearlings	 Subadults
Percent of total population 1			
Interbirth interval (IBI)	-0.800 0.02	-0.438 0.16	-0.099 0.58
Generation length (G)	-0.778 0.02	-0.405 0.18	-0.052 0.54
Cub litter size (C/L)	0.868 0.006	0.195 0.34	-0.228 0.31
Productivity (C/L/IBI)	0.877 0.005	0.395 0.19	-0.015 0.48
Reproductive vigor index (RVI)	0.879 0.005	0.394 0.38	-0.001 0.50
Number per adult female 2			
Interbirth interval (IBI)	-0.754 0.03	-0.324 0.24	-0.084 0.43
Generation length (G)	-0.714 0.04	-0.294 0.26	-0.001 0.50
Cub litter size (C/L)	0.742 0.03	0.086 0.43	-0.220 0.68
Productivity (C/L/IBI)	0.809 0.01	0.279 0.27	-0.010 0.49
Reproductive vigor index (RVI)	0.809 0.01	0.279 0.27	-0.004 0.50

* Values given are r (above) and P:1t (below). Data from Tables 3:1 and 3:5.

[1] E.g., percent cubs in the population (#C/N).

[2] E.g., cubs per adult female (#C/AdF).

habitats where bears aggregated in large numbers to feed, and where adult sex ratios were about 45% males (Table 3:5). Although (a) aggregation might explain why those rates of mortality are much higher than rates calculated by comparing cub vs. yearling litter sizes in other populations, (b) this difference in mortality rates could instead be an artifact of either sample size (Glenn et al. 1976) or of methodology (Stringham 1980), as shall be described below.

Assessing survivorship by comparing sizes of litters at successive ages is most reliable where the same litters are compared at both ages, or at least where all belong to the same cohort. However, that is rarely done. In the other populations for which cub and yearling litter size data are available, few litters were individually known. Cub litters were compared with yearling litters present during the same year, and thus belonging to the previous cohort rather than to the same one. As data on Yellowstone grizzlies clearly reveals, mean cub litter size can vary as much among cohorts as among populations. So yearling litter size during any year could be smaller than cub litter size even in lieu of mortality; or, it could be larger. Furthermore, even if one were to compare litter sizes at successive ages only within the same cohorts, mortality rate could be seriously underestimated unless losses of entire litters are documented thoroughly (Stringham 1980). For example, if smaller litters have elevated attrition rates, mean litter size at yearling age could actually be larger than mean size at cub age (see Tait 1980). Finally, when litter sizes are assessed by aerial survey, litters of yearlings are sometimes indistinguishable from litters of older offspring still associated with their dam (Glenn et al. 1976). These potential biases might account for the fact that when one considers differences in sizes not just of the 13 known litters at McNeil, but of all 110 litters observed on that portion of the Alaska Peninsula, the apparent mortality rate is not 38% but only 13%.

If one is to compare relative sizes of cub vs. yearling litters at McNeil with those in other populations, it should be done on the same basis for all--unavoidably, unidentified litters. Comparative data on cub and yearling litter sizes is available from 10 populations (Table 7:3). Unweighted mean litter size change was +1% for 5 hunted populations and -5% for 6 protected populations (using the -13% figure for McNeil). However, if means are weighted by sample size (where known), litter size declines are over twice as high in hunted (-9%) populations as in protected (-4%) populations. Unweighted mean litter size declines for 2 populations with <6% adult males (KI & CBL) is -9.5%, contrasted to -0.25% in 4 populations with >21% adult males (MR, SYT, EBR, WBR). If one assumes that proportion of adult males is high in all populations except KI and CBL, where it is known to be low, the unweighted mean decline for these latter populations is still less than |-1%|.

Therefore, _if_ cub mortality rates between ages 0.5 - 1.5 years could be reduced by hunting adult males, these comparisons are not sensitive enough to reveal that. In fact, these results suggest just the opposite: that cub mortality rates are higher in populations

Table 7:3. Respective sizes of cub and yearling litters in grizzly populations.*

Population	Cub (C)	Yearling (Y)	Difference (C-Y)/C = %	Difference unw. $\bar{x}$	Difference ssw. $\bar{x}^1$
HUNTED					
Lake Becharof (Troyer, cited by Faro 1977)	2.0	2.0	0		
Kodiak Island (KI) (Hensel et al. 1969)	2.23 (98)	2.00 (103)	-10 (201)		
Chignik-Black Lakes (CBL) (Glenn 1973)	2.3	2.1	- 9 (342)		
Eastern Brooks Range (Reynolds 1976)(EBR)	1.8 (13)	2.0 (7)	+10 (20)		
Western Brooks Range (Renolds 1980, in press)(WBR)	1.98	2.25	+14		
Mean				+1 (5)	-9 (563)

Table 7:3. (Continued)

Population	Cub (C)	Yearling (Y)	Difference		
			(C-Y)/C = %	unw. $\overline{x}$	ssw. $\overline{x}$
PROTECTED					
McNeil River (MR) (Glenn et al. 1976)	2.1	1.8[2]	-13 (110)		
Southwestern Yukon Territory (SYT) (Pearson 1975)	1.7 (11)	1.5 (11)	-12 (22)		
Glacier National Park, USA (Martinka 1974)	1.7 (35)	1.8 (30)	+ 6 (65)		
Glacier National Park, Canada (Mundy & Flook 1973)	2.00 (108)	1.93 (45)	-4 (153)		
Denali National Park (Dean 1976)	1.81	1.85	+ 2 (63)		
Katmai National Monument (Troyer, cited by Faro 1977)	2.0	1.8	-10		
Mean				-5 (6)	-4 (413)

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* Values given are the mean and number of litters censused ( ), if known.

[1] Unw. $\overline{x}$ = unweighted mean, n = #populations; ssw. $\overline{x}$ = sample size weighted mean, n = #litters.

[2] Litters aged 1.5 - 3.5 years.

where density of adult males has been seriously reduced by hunting. That coincides with evidence for black bears that under some conditions, killing resident adult males might increase cub mortality (Rogers 1976; see Chapter 9:III).

We also do not know the extent to which these declines in litter size between ages 0.5 - 1.5 years represent mortality. Some young may have become independent before they were censused as yearlings. Johnson & LeRoux (1973) reported that a cub orphaned at age 7 months survived until the next year, when it was shot. Other orphaned cubs are adopted, as has been documented at both YNP and McNeil (e.g., Erickson & Miller 1963; Erickson 1964; Russel 1967; J. Craighead et al. 1969, pers. comm; F. Craighead [in Herrero 1972: 82]; Bledsoe 1975). Indeed, yearling litters in the Eastern and Western Brooks Range averaged larger than cub litters. It remains to be determined whether these larger yearling litter sizes represent migration, adoption, or just sampling error (e.g., due to annual fluctuations in mean cub litter size and comparison across rather than within cohorts, or higher mortality among small litters).

7:II.B. Relative Correlations for Reproductive Parameters vs. Environmental and Infrastructural Factors

Table 5:1 presented correlations between parameters of reproduction relative to approximate latitude and habitat type (coastal vs. inland) for each of 10 grizzly populations. Table 5:2 presented such correlations relative to population density--another index of food supply and nutrient-energy balance--in each of 7 habitats. Comparable correlations are presented here in Table 7:4 on just those same 7 grizzly populations for which infrastructure was also documented. That is done to facilitate comparisons of correlations between reproductive parameters vs. (a) indices of food supply and nutrient-energy balance with correlations vs. (b) proportions of adult males in those populations.

Percent adult males is correlated with percent cubs more strongly than are latitude and habitat type, either separately or jointly. This is apparently not an artifact due to correlating percentages of 2 age-classes from within the same population (see Section III.A.2); for the correlations between percent adult males vs. ratios of immatures per adult female were comparable.

Percent adult males is also more strongly correlated with all the other reproductive parameters than is either latitude, habitat type, or population density (even though the seemingly anomalous density datum from Kodiak Island was excluded). Only when latitude and habitat type are taken into account together are the correlations between reproductive parameters vs. those environmental factors stronger than the correlations vs. densities of adult males. This difference cannot be attributed to inflation of the multiple correlation coefficients due to the small sample size of 7 populations. For the difference is preserved after the coefficients have been deflated using Wherry's (1931) formula, as recommended by Schmitt et al. (1977). That formula is:

Table 7:4. Reproductive and infrastructural parameters correlated to proportion of adult males and to latitude, habitat type, and population density in 7 grizzly populations.*

Parameter	Percent Adult Males	Latitude (Lat)	Habitat Type (Hab)	Lat Hab	Population Density	Lat[1] Hab Den
Interbirth interval	0.859	0.781	0.791	0.979	-0.602	±0.979
(IBI)	0.007	0.02	0.02	0.001	0.08	0.005
	(0.828)[2]			(0.968)		(±0.958)
Generation length	0.909	0.751	0.755	0.938	-0.578	±0.938
(G)	0.002	0.03	0.03	0.007	0.09	0.04
	(0.890)			(0.905)		(±0.871)
Cub litter size	-0.794	-0.653	-0.711	-0.850	0.526	±0.853
(C/L)	0.02	0.06	0.04	0.04	0.09	0.11
	(-0.746)			(-0.764)		(±0.675)
Productivity	-0.858	-0.734	-0.800	-0.957	0.616	±0.957
(C/L/IBI)	0.007	0.03	0.02	0.004	0.07	0.02
	(-0.827)			(-0.935)		(±0.912)
Reproductive vigor	-0.893	-0.732	-0.790	-0.949	0.604	±0.950
index (RVI)	0.003	0.03	0.02	0.005	0.08	0.025
	(-0.870)			(-0.922)		(±0.897)
Percent cubs	-0.904	-0.262	-0.843	-0.848	0.597	±0.849
(#C/N)	0.01	0.31	0.02	0.07	0.11	0.19
	(-0.884)			(-0.761)		(±0.665)
Cubs/adult female	-0.889	-0.271	-0.871	-0.876	0.824	±0.932
(#C/AdF)	0.01	0.30	0.01	0.06	0.02	0.10
	(-0.865)			(-0.807)		(±0.859)

Table 7:4. (Continued)

Parameter	Percent Adult Males	Latitude (Lat)	Habitat Type (Hab)	Lat Hab	Population Density	Lat Hab Den
Percent yearlings (#Y/N)	-0.571 0.12	-0.177 0.36	-0.676 0.07	-0.672 0.20	0.854 0.02	±0.864 0.18
Yearlings/adult female (Y/AdF)	-0.425 0.20	-0.138 0.40	-0.537 0.14	-0.538 0.30	0.811 0.03	±0.811 0.23
Percent subadults (#SAd/N)	-0.263 0.31	-0.030 0.48	-0.371 0.23	-0.374 0.40	0.027 0.48	±0.479 0.45
Subadults/adult female (#SAd/AdF)	-0.160 0.38	-0.072 0.45	-0.295 0.29	-0.295 0.44	0.374 0.233	±0.143 0.47
Percent adult[3] females (#AdF/N)	0.539 0.21	0.436 0.33	0.366 0.42	0.502 0.28	-0.537 0.11	±0.621 0.64
Percent adult[3] males (#AdM/N)		0.428 0.34	0.911 0.004	0.927 0.01	-0.620 0.07	±0.927 0.085
Adult males/adult[3] female (#AdM/AdF)		0.263 0.57	0.901 0.006	0.901 0.02	-0.551 0.20	±0.907 0.12
Adult sex ratio[3] (#AdM/#Ad)		0.280 0.54	0.951 0.001	0.951 0.005	-0.544 0.21	±0.964 0.03
Percent adults[3] (#Ad/N)		0.483 0.27	0.817 0.025	0.856 0.04	-0.664 0.10	±0.747 0.20

* Data from Tables 3:1, 3:5, and 4:1.

[1] Since density tended to be negatively correlated with latitude and habitat type, multiple correlations involving all 3 of those variables had to be expressed as ±R.

[2] Deflated correlation coefficients are given in parentheses below significance level for the (inflated) coefficient obtained directly from the Pearson Product Moment calculation.

[3] A 2-tailed significance level, used because theory did not yield predictions of whether abundance or sex ratio of adults would be positively or negatively correlated with latitude or habitat type.

$$\text{rho}^2 = [1 - (n-1)/(n-p-1)] * (1-R^2)$$

where rho is the deflated correlation coefficient and R the inflated one, n is sample size, and p is number of independent variables (Table 7:4). After deflation of correlation coefficients, density, latitude, and habitat type together seem to account for at least 45% of variance in each univariate reproductive parameter, and 80% of variance in the Reproductive Vigor Index, which encompasses all of the other reproductive parameters. The biological significance of these findings shall be discussed in Section III.B. First, however, let us consider evidence that these results were _not_ seriously biased by either of 2 potential sources of statistical artifact.

7:III. _DISCUSSION_

7:III.A. _Possible Biases_

There are 2 potential sources of bias in the way parameters of reproduction were regressed against relative abundances of adults or adult sex ratio: (1) autocorrelation and (2) percentages of different classes within a population. However, it seems that neither source of bias had a detectable effect on these particular results.

7:III.A.1. _Autocorrelation_

There is an element of autocorrelation in the relationships between (a) ratios of immatures vs. ratios of adult males per adult female, or (b) percents of immatures vs. percent adult males. For example, with

#C/AdF = f(#AdM/AdF)   or   #C/N = f(#AdM/N)

either abundance of adult females (#AdF) or total population size (N) is in the denominator on both sides of the equation, tending to produce a positive correlation overall. So, even the strong negative correlations found for these relationships could be underestimates.

7:III.A.2. Percentages

However, comparison on the basis of percentages of immatures vs. adults in the population (#C/N vs. #AdM/N) would tend to counter effects of autocorrelation by tending to exaggerate negativity of correlations. That might help to explain why the correlation for C/N vs. #AdM/N was more negative than that between C/AdF vs. #AdM/AdF.

The potential for exaggerating negativity of correlations between percents of 2 age-sex classes (e.g., #C/N vs. #AdM/N) in the population stems from the fact that in populations where the percentage of adults is high, combined percentages of all immatures must be low. For example, if 40% of the bears in a population are adults, 60% must be immatures; if 30% are adults, 70% are immatures. So, for purely mathematical reasons, there tend to be negative correlations between percents of different age- or sex-classes within a population.

Whether that tendency is realized, of course, depends upon how large a proportion of the total population is encompassed within the 2 age-sex classes chosen for intercorrelation tests. If (1) their combined proportion in the population is small, and (2) if their combined variation is a small fraction that of the whole population, then bias should also be small. Percents of immatures and adult females have standard deviations ranging from ±4.4 to ±6.4, compared to ±10.1 for adult males. So any bias should be small for adult males and smaller still for adult females.

In conclusion, even if exact magnitudes of these negative correlations have been perturbated by statitical artifacts, the consistency among the negative correlations is almost unanimous. All that can be said at this point is that (a) any biases are probably negligible, and (b) comparisons based on ratios of bears in each age-sex class per adult female (e.g., #C/AdF vs. #AdM/AdF) are probably more reliable and biological revealing than those per total population size (e.g., #C/N vs. #AdM/N).

7:III.B. Relative Impacts on Demography by Environmental vs. Infrastructural Factors

Negative correlations between parameters of reproduction vs. abundance of adults, particularly adult males, are consistent with the hypothesis of density dependency. But correlation does not, of course, demonstrate causation. So it is to the question of causation that we now turn. As a first step, let us consider the possibility that the negative correlations between reproductive parameters vs. adult abundance are artifacts of correlations between both (a) reproduction and (b) adult abundance vs. various environmental factors.

Correlations between population density, latitude, and habitat type vs. percents of adults and adult sex ratio were given in Table 7:4. Adult males were scarcest in the coastal populations at Kodiak Island and Chignik-Black Lakes (Table 3:5), presumably due to the intense hunting pressure there. By contrast, adult males were relatively abundant in the coastal population at McNeil River Game Sanctuary, where hunting pressure was lighter and focused mainly on those bears that moved outside of the protected area (Faro, pers. comm.).

Proportions of adults in the inland populations were positively correlated with latitude, tending to be particularly high in habitats above 65 degrees north latitude. That is due partly to the lower rates of harvest there as well as to the low rates of reproduction which by itself could reduce proportions of cubs and yearlings in a population, particularly relative to abundance of adult females.

Thus, these correlations between abundances of adults, especially adult males, vs. habitat type, latitude, and density are real. But they seem to be artifacts of hunting, rather than inherent in the ecology of the species. The 2 unprotected coastal populations are heavily hunted because good food supplies for the bears and mild climates promote high rates of reproduction and dense populations of large body size. Conversely, sparce population density, small body size, and inaccessibility (due largely to distance), tend to reduce harvest pressure on the northern-most (inland) populations. So it is harvest pressure, rather than habitat type or latitude or density per se, which could best be used to predict relative abundance of adults and adult sex ratio. Furthermore, latitude and habitat type statistically account for at least 81% of variance in the proportion of adult males and 90% of that in adult sex ratio. Hence, these relationships between latitude and habitat type vs. (a) hunting pressure and (b) reproduction, statistically account for most of the negative correlation between reproductive parameters vs. abundances of adults, especially adult males.

Is this evidence that abundances of adults exerted little density dependent inhibition on reproduction (or recruitment), compared to the effects of latitude, habitat type, and perhaps other environmental factors? Possibly, but not necessarily so, since correlation can obscure causation. The proportion of variation in Y "accounted for" by X in a correlational sense can be far stronger than the proportion accounted for in a causal sense. That becomes obvious when one considers an hypothetical example:

> When one claps one's hands, the resultant sound might be equally correlated with the movement of either hand, even though both contribute to producing the clap. So too, if 10,000 people in a stadium clap in unison, the clapping of each person could cause only about 1/10,000th of the total sound; yet, his/her hand movements could be very highly correlated with the total sound

> pulse, and could thus <u>correlationally</u> account for nearly all the sound.

Although a distinction between correlation vs. causation is commonly made in the sense of 2 events occuring in parallel merely fortuitously, rather than as the result of either causing the other or both being responses to some third event, this second kind of distinction between correlation vs. causation is seldom addressed and often ignored in interpretation of determination coefficients. Thus, in this case, differences among populations in reproductive rate might be consequences of differences in both environmental and infrasturctural-density differences. If infrastructural effects simply compounded those of latitude and habitat type, the respective contributions by those infrastructural vs. environmental factors would not be fully distinguishable statistically.

Maturation to puberty and first reproduction is slower among black bears in Alaska (Rausch 1961) and Montana (Jonkel & Cowan 1971), than among those in Michigan (Erickson & Nellor 1964). Noting this, Pearson (1975:38) stated:

> Both authors ascribed this late minimum breeding age to nutritive status. However, it is possible that the heavier mortality from hunting in Michigan elicited some compensatory natality mechanism that resulted in earlier successful breeding.

An obvious hypothesis is that any such compensatory mechanism is controlled by abundance of adult males. So too, the fact that abundance of adult males was higher at McNeil River that at the other 2 coastal grizzly populations might help to account for generation length at McNeil being about 1 year longer than at those other coastal populations. The high density of grizzlies which regularly aggregate at McNeil Falls to feed (on salmon) was paralleled only by the density of grizzlies once regularly feeding at garbage dumps in YNP. Levels of social strife seemed correspondingly higher there than in habitats where the bears were normally more dispersed (Hornocker 1962; Stokes 1970; Stonorov & Stokes 1972; Egbert & Luque 1975; Bledsoe 1975). Under those conditions of high (a) density, (b) strife, and (c) adult male abundance, dams and their unweaned offspring seemed especially vulnerable to aggression by adult males.

Evidence of maturation retardation by social domination and strife has been obtained for numerous species of mammals (e.g., see Davis 1964; Christian 1980; Snyder 1962, 1976; Sadlier 1969) and other vertebrates, for instance the Platyfish (*Xiphophorus maculatus*; Sohn 1977). Some authors have long attributed socially retarded maturation to elevation of the Selye General Adaptation Symdrome (GAS), or so-called physiological "stress" or "distress" (e.g., Selye 1956, 1976). Another possible mechanism for social control of maturation rate is the so-called "Vandenbergh Effect" (Vandenbergh 1967, 1969, 1973), wherein maturation can be retarded by urine-borne pheromones of same-sex adults or accelerated by such pheromones from opposite-sex adults. This has been demonstrated in several species of rodents and domestic ungulates (e.g., see Izard & Vandenbergh 1982). Whether it occurs in any carnivores is apparently not known. But there is no indication that it could explain retarded maturation at McNeil. For the higher proportion of adult males there than in the other coastal populations would be likely to accelerate, not retard, maturation by females if the Vandenbergh Effect were the mechanism of influence. So strife-induced arousal of physiological distress seems a more likely explanation.

Rogers (1976, 1977) observed no delay of maturation by 4 immature black bears raised in captivity with adults who dominated them. However, that does not preclude the possibility that adult males stress immatures under quite different (natural) social and ecological conditions. For example, familiarity with cage-mates could greatly reduce social strife, fear, and anxiety, (see Stonorov & Stokes 1972; Egbert & Stokes 1976) and thus reduce level of the G.A.S. That would be less likely under natural conditions, especially where adult males attempt to evict immatures from prime foraging sites or to exile them from local habitat or to kill them.

The relationship between cub litter size and strife also needs consideration. Despite the slow rate of maturation at McNeil, cub litter size was about as large as at the other 2 coastal populations (2.1 vs. 2.2 C/L). Apparently, strife exerted little if any effect on litter size prenatally or early postnatally, prior to aggregation at McNeil, where censusing occurred. However, litter size was reduced thereafter, presumably by strife, especially aggression from adult males, as hypothesized by Glenn et al. (1976). Recall that reduction in litter size between cub vs. yearling ages was 38% among the 13 individually known litters, although only 13% among all 110 litters sampled (Section II.A.2., above).

As shall be discussed at length in following chapters, whelping rate and level might also be affected by strife both pre- and postnatally. Reduction in litter size manifests only partial-litter loss, not whole-litter loss. Yet, data from other species on prenatal mortality of offspring in relation to social strife (e.g., the "Bruce Effect"; see Bruce 1959; Schwagmeyer 1980; Berger 1983) suggests that whole litter loss is more likely than partial litter loss prenatally. Furthermore, infanticide theory (Hrdy 1979) suggests that adult males would gain more from eliminating whole litters than from just eliminating some of the cubs, particularly since whole litter loss may be required to shorten the interval until the dam's next fertile estrus and thereby shorten delay until the infanticidal male can mate with her (Chapter 11:III.B.2.e). Vulnerability of neonates might also favor whole litter loss during the first several months postpartum (e.g., see Reynolds 1976, 1980, in press). But vulnerability would decline thereafter as cubs gain in speed, agility, and wariness (see Taylor et al., in press; Chapter 11:III.B.2.e). Those considerations lead to the prediction of strife initially (i.e., prenatally and early postnatally) reducing apparent whelping rate and level more than litter size, whereas litter size would be affected increasingly as the litters mature.

If whole litter loss occurred prior to censusing, production of the litter could remain undetected by observers, and thus give the impression that interbirth interval was longer than actual. That, along with retarded maturation, could explain why interbirth intervals at McNeil were longer than in the other coastal populations.

7:III.C. Comparison Among Black Bear Populations

Infrastructural data on most black bear populations is too sparce for one to compare among them as has been done here for grizzly populations. The main exceptions are the 2 Idaho black bear populations compared by Beecham (1980a,b). The population at Council was subjected to heavier hunting pressure than that at Lowell. Proportions of adults and the ratio of adult males per adult female seemed lower in the more heavily hunted population; but the ratio of immatures per adult female and total population density seemed higher at Council (Table 7:5). According to Beecham, this difference in relative abundance of adult males probably accounts in large measure for the fact that the amount of ingress and egress by subadults, especially males, was greater at Council. That would be consistent with findings on social behavior in other black bear populations (Kemp 1976; Rogers 1976, 1977, 1983; Young & Ruff 1982; Ruff, in prep).

The fact that net ingress by subadults was higher or net egress lower at Council apparently cannot explain why the ratio of immatures per adult female was higher there. If the higher ratio was due primarily to differences in net ingress or egress, one would expect the ratio to have been much higher for male immatures than for females, since males disperse farther and travel more. On the contrary, sex ratio among immatures seemed lower at Council.

Table 7:5. Comparison between 2 Idaho black bear populations.*

Parameter	Council (C)	Lowell (L)	Difference (C-L)/C = %
Hunting Pressure	heavy	light	
Population density ($N/100\ km^2$)	47.6	43.5	+ 8.6
Percent adults (#Ad/N)	53	71	-34.0
Percent adult females (#AdF/N)	32	36	-12.5
Percent adult males (#AdM/N)	21	35	-66.7
Adult males per adult female (#AdM/AdF)	0.66	0.97	-47.3
Adult sex ratio (%MAd = #AdM/#Ad)	40	49	-22.5
Immature sex ratio (%MIm = #ImM/#Im)	64	69	- 7.8
Immatures per adult female (Im/AdF)			
males	0.93	0.56	+39.8
females	0.53	0.25	+52.8
total	1.46	0.81	+44.5
Cub litter size (C/L)	1.90	1.65	+13.2 P:2t < 0.10*
Age at puberty (AP)	4.25	4.50	+ 5.9 P:2t < 0.10*
Growth rate	faster	slower	

* Data and t-test results from Beecham 1980a,b.

Furthermore, the infrastructural and density data provided by Beecham was calculated in a way designed to minimize bias due to transient visitation by subadults.

Thus, the higher ratio of immatures per adult female at Council may instead be attributable to differences in rates of reproduction and survivorship as a consequence of differences in habitat quality. That is the factor to which Beecham attributes the higher mean litter size and rates of growth and maturation at Council.

It is not clear why Beecham considers differences in abundance of adult males, other biosocial factors, or (other) impacts of hunting, to have had negligible effect on reproduction and survivorship. Perhaps differences in habitat quality were so great as to obviously dominate differences in biosocial influences--as was the case with Roger's observations on Minnesota black bears (Chapter 10:II.A). For example, differences in food supply may have had much more influence than differences in bear density and mass on food supply per bear and per unit bear mass. Or effects of adult male abundance may have obviously had much less impact than food supply on rates and intensities of intraspecific strife and killing of immatures. But so far, no documentation has been provided for those Idaho populations on (a) differences in habitat quality, for instance in terms of food supply or climate, or on (b) relative impacts by habitat quality vs. biosocial factors vs. hunting impacts. So a reviewer cannot yet exclude the possibility that part of the difference in reproduction and survivorship between the 2 populations was due to differences in relative abundances of adults, especially adult males.

7:IV. SUMMARY

1) Comparison among 8 grizzly populations reveals that those with the highest proportions of adults, relative to immatures, tend to have the slowest rates of maturation to weaning and first whelping, judging from correlations with interbirth interval and generation length. They also tend to have the smallest cub litter sizes, and thus the lowest proportions of cubs, productivities (cubs per year per adult female), and reproductive vigors (combined contributions by reproductive parameters to population growth rate). These correlations were higher for adult males than for adult females, partly because proportion of adult males was more variable and partly because adult males exert a greater per capita density-dependent impact.

2) Available data provide no indication that cub recruitment rate between ages 0.5-1.5 years is any higher in populations where adult males are scarce or hunting pressure high; so hunting adult males may not necessarily increase offspring recruitment. Specialized conditions under which it is most likely to do so are discussed in Chapter 11:IV.

3) Reproductive parameters were correlated with percent adult males in each population more strongly than with either latitude or habitat type (coastal vs. inland). Even when latitude and habitat

type are considered together, their correlations vs. reproductive parameters average only slightly stronger than correlations of percent adult males vs. reproductive parameters.

4) Variations among populations in percent adult males seem due largely to hunting impacts. Hunting pressure is related to latitude and habitat type for each population according to accessibility and productivity (number per year and size of harvestable bears). Thus, there is a negative correlation between percent adult males vs. latitude and habitat type.

5) As a result, relative strengths of correlation coefficients between reproductive parameters vs. (a) percent adult males, and vs. (b) latitude and habitat type, do not fully reveal the relative strengths of their impacts.

6) Part of the correlation between reproduction vs. percent adult males could be a spurious consequence of the positive correlation between reproduction vs. latitude and habitat type. But how large a part that is cannot yet be quantified.

7) The fact that female generation length at McNeil was about 1 year longer than at the other 2 coastal grizzly populations, despite abundant food, is probably attributable largely to social strife. Strife was apparently greater at McNeil because feeding aggregations were denser and adult males more abundant there than in the other 2 populations. Elevated social strife apparently had less effect on cub litter size prenatally and early postnatally than it did once the bears began to aggregate at McNeil Falls and after they left the Falls

each year. Whole-litter loss is likely to have been more common prenatally and early postnatally than litter size reduction, whereas the reverse would have been true subsequently. That may reflect shifts in both the mechanisms of influence on litters (prenatally: physiological distress of the dam; postnatally: physiological distress of dam and cubs and direct aggression against them) and age-related vulnerability of the litter. As cubs mature, their increasing wariness, speed, and agility reduce their vulnerabiliy to conspecifics (see Taylor et al., in press).

RESPONSES BY GRIZZLY BEAR POPULATION DYNAMICS TO CERTAIN ENVIRONMENTAL AND BIOSOCIAL FACTORS

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Stephen Frederick Stringham
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CHAPTER 8

YELLOWSTONE GRIZZLIES: RESULTS

This chapter presents results of tests made to determine, for Yellowstone grizzlies, whether or not rates of reproduction and recruitment are inversely dependent upon density or biomass of the entire population or of any age-sex class--i.e., whether they are "density dependent." Results of comparable tests for Minnesota black bears are presented in Chapter 10:II.

In Chapter 5, rates of reproduction and recruitment for Yellowstone grizzlies were evaluated in terms of indices for total food supply and for supply per bear or per unit bear-mass. If rates of reproduction and recruitment were completely density independent, then these rates should not have been correlated with (a) supply per bear or per unit bear-mass any more strongly than with (b) total food supply per se. However, judging from available indices, correlations vs. total supply were weaker on average than those vs. supply per bear; correlations vs. supply per unit bear mass were the strongest of all.

$$r: \quad FS < FS/N < FS/BM$$

Although the differences in magnitudes of the correlation coefficients between the 3 indices are small and variable, overall they are quite clear. This is at least tentative evidence of density dependence among Yellowstone grizzlies --evidence that amount of food received per bear and per unit bear-mass depended not only upon variation in food supply per se, but also on variations in population density and biomass.

That substantiates findings by Schaffer (1978, 1983), McCullough (1981), and Stringham (1983) on this same population. Schaffer found negative correlations between the proportion of adult females in year t producing cub litters in t+1 and mean size of these litters vs. density of adults in year t (prenatally). By contrast, McCullough (1981) found negative correlations between proportion of adult females in year t producing litters <u>then</u> and mean size of their litters then (postnatally).

McCullough also found negative correlations between postnatal density of adults vs. cub sex ratio, and ratios of immatures per adult. These ratios per adult refer to densities of recruits (cohort sizes) at ages 0.5-4.5 relative to density of adults postnatally. Negligible correlation was found between ratios of immatures at ages 1.5-4.5 per adult <u>concurrently</u> vs. density of adults concurrently. McCullough also reported a positive correlation between adult sex ratio vs. adult density. When adults were abundant, most were males; when they were scarce, most were females. Although densities of male and female adults tended to increase together ($r = 0.669$, $P:2t=0.02$), density of adult females varied less than that of adult males. On average, males predominated among cubs, whereas females predominated among adults. This decline in sex ratio with advancing age was attributed to a disproportionate mortality rate among male immatures--contrary to the opinion expressed by J. Craighead et al.

(1974) that it was due primarily to disproportionate mortality rate among male adults.

McCullough concluded that the inverse relationships between cub density and sex ratio vs. adult density and sex ratio would tend to regulate the population. However, because of the approximately 5-year lag between infancy and adulthood, regulation would produce not a stable mean, but osciallation with a period of 2 generation lengths, or about 10 years in this population. For example, if density and sex ratio of adults were high in year t, density and sex ratio of cubs would be low, leading to low density and sex ratio of adults 1 generation later (t+5), and thus high density and sex ratio of cubs then, leading once more to high density and sex ratio of adults after another generation (t+10). The suggestion was made that these oscillations could be dampened by selective harvest of the adult males at a level where density and perhaps even age-structure might stabilize.

Although the analyses of the Yellowstone data presented here were begun before I learned of those by Schaffer and McCullough (see Stringham 1983), these can be thought of as refining and extending their insights. That was done in 3 ways:

(1) As described above, Schaffer presented relationships between 2 parameters of reproduction vs. _prenatal_ density of adults. McCullough presented relationships between several parameters of reproduction and recruitment vs. _postnatal_ and _concurrent_ densities of adults, as well as relationships between a single parameter vs. densities of male and

female adults, postnatally and concurrently. Some relationships were also tested relative to population density, with or without inclusion of various immature age-classes. By contrast, here, all parameters are tested for relationships vs. concurrent, pre-, post-, and circumnatal densities and biomasses of all age classes, individually and in groups.

(2) A number of additional parameters are evaluated here.

(3) Different mathematical models are fit to the data--models which seem more appropriate on both statistical and biological grounds. Schaffer fit only linear models. McCullough also fit linear models; but those of form #R/Ad vs. #Ad (#R = density of recruits at the given age), were then transformed into polynomials for parabolic curves.

$$\#R/Ad = a - b*\#Ad \qquad \text{Linear}$$

$$\text{to} \qquad \#R = a*\#Ad - b*\#Ad^2 \qquad \text{Parabolic}$$

Although both the linear and parabolic forms of this relationship have high coefficients of determination and confidence level, that seems to be artifactual. Indeed, they do not appear to fit the data as closely as do the alternative models presented here (see Chapter 9:I.C.1). Nor do the parabolic models seem as compatible with the previously discussed results on how parameters of reproduction and recruitment are related to food supply per bear and per unit bear mass.

Derivation of appropriate models shall now be done in 3 steps. (1) Empirical results: Data are fit by regression models, some of which are applicable only over that range of values (below).

(2) Interpolation or extrapolation of the models to ranges of values not observed, and any modifications that necessitates (Section 8:II.B.). (3) Derivation of theoretical models based on simultaneous responses to both food supply and biomass/density (Chapter 13:II).

To begin with, then, recall that cub litter size was about equally sensitive to each unit of change in food supply, supply per bear, or per unit bear mass, at all levels of those food supply and nutrient-energy balance indices; that is, the relationships were approximately linear. So too, cub litter size seems linearly related to density and biomass per se, as also shown by Schaffer (1978, 1983) and McCullough (1981):

$$\#C/L = a - b*(N)$$

By contrast, sensitivity of the other parameters of reproduction and recruitment decline as the levels of food supply, supply per bear, and per unit bear mass increase. In Chapter 5, these relationships were approximated with semi-logarithmic models (e.g., #C vs. FS/N). Consequently, semi-logarithmic models are used here too in corresponding regressions against just density or biomass. For example:

$$\begin{aligned}\#C &= p + q*\log(FS/N)\\ &= p + q*\log(FS) - q*\log(N)\\ &= p' - q*\log(N)\end{aligned}$$

where $p' = p + q*\log(FS)$, assuming that mean food supply is constant and that variations in food supply are uncorrelated with variations in density. Equations for biomass are comparable. Since negative correlations are predicted, tests of significance are 1-tailed.

8:I. DENSITY AND BIOMASS OF THE POPULATION AND OF IMMATURES

As expected from the relationships between parameters of reproduction and recruitment vs. food supply per bear and per unit bear mass, these parameters tend to be negatively correlated with density and biomass. Correlations with total population density are so weak that their confidence levels are too low to be reliable, except in combination. But correlations with total population biomass are stronger, and most have significance levels of $P{:}1t<0.05$ (Table 8:1).

By contrast, neither density nor biomass of just immatures was consistently, negatively correlated with parameters of reproduction and recruitment, suggesting that density and biomass of immatures had little impact on those parameters. This result is obtained irregardless of whether one considers density and biomass of all immatures together or only of specific age-classes (e.g., ages 0.5-4.5 or 2.5-4.5).

That result helps to explain why parameters of reproduction and recruitment are more strongly correlated with population biomass than with population density. Density "weights" a cub as equivalent to a yearling or an older immature or an adult. By contrast, biomass "weights" the most massive bears most heavily. The relative lack of correlation between parameters of reproduction and recruitment vs.

Table 8:1. Reproductive parameters correlated to population density and biomass for the Yellowstone grizzly population, 1959-70.*

			Adult Density										
			Outliers										
	Total	Total	Present			Absent [1]			% Male	Adult			
Parameter	Density	Biomass	Total	Males	Females	Total	Males	Females	Adults	Biomass	Pr	Po	Cr[2]
Reproductive [3] factor	-0.135 0.35	-0.563 0.04	-0.646 0.02	-0.662 0.01	-0.394 0.23	-0.954 0.0001	-0.975 0.0001	-0.361 0.15	-0.704 0.008	-0.964 0.0001	x		
Cub litter size	-0.241 0.24	-0.562 0.04	-0.630 0.02	-0.607 0.02	-0.562 0.04	-0.857 0.001	-0.830 0.002	-0.467 0.09	-0.590 0.04	-0.850 0.001	x		
Whelping rate	-0.124 0.35	-0.507 0.04	-0.530 0.03	-0.537 0.04	-0.501 0.05	-0.674 0.01	-0.704 0.01	-0.725 0.005	-0.541 0.04	-0.689 0.01		x	
Whelping level	-0.093 0.39	-0.366 0.12	-0.332 0.15	-0.360 0.12	-0.261 0.21	-0.560 0.04	-0.586 0.03	-0.572 0.03	-0.380 0.11	-0.580 0.03		x	
Interbirth interval	0.269 0.78	-0.335 0.16	-0.540 0.04	-0.569 0.03	-0.160 0.32	-0.501 0.08	-0.578 0.05	-0.204 0.30	-0.592 0.03	-0.519 0.08			x
Cub sex ratio (%MC)	-0.436 0.09	-0.744 0.004	-0.548 0.04	-0.614 0.02	-0.130 0.35	-0.598 0.04	-0.676 0.02	-0.585 0.025	-0.674 0.01	-0.623 0.04			x
#Male cubs	-0.500 0.06	-0.796 0.002	-0.593 0.03	-0.639 0.025	-0.261 0.22	-0.685 0.02	-0.734 0.01	-0.588 0.025	-0.678 0.01	-0.701 0.02			x
#Female cubs	0.269 0.21	0.490 0.06	0.362 0.14	0.435 0.09	-0.008 0.51	0.268 0.24	0.365 0.17	0.525 0.04	0.504 0.06	0.298 0.22			x
#Cubs	-0.488 0.07	-0.745 0.004	-0.556 0.04	-0.575 0.03	-0.336 0.16	-0.714 0.015	-0.727 0.01	-0.480 0.10	-0.587 0.03	-0.719 0.015			x

Table 8:1. (Continued)

* Values given are r and P:1t. (Data from Tables 3:2, 3:6, and 4:5).

[1] Data omitted as outliers were 1960 for adult males, total adults, and adult sex ratio, as well as adult biomass. For adult females, the 1960 datum was omitted only with regard to the compound reproductive factor and to cub litter size; for other parameters the 1967 dataum was omitted.

[2] Pr = prenatal, Po = postnatal, Cr = circumnatal--referring to density or biomass of the total population or of just adults.

[3] Correlations between density and biomass vs. the reproductive factor and cub litter size are approximately linear; all those other correlations vs. parameters of reproduction and recruitment are approximately semi-logarithmic (e.g., #L/AdF = a - b*ln[N]).

population density, despite the strong correlations vs. population biomass, stems from the confounding or masking effects from variations in density of immatures.

8:II. DENSITY AND BIOMASS OF ADULTS

8:II.A. Empirical Results

Variance in adult biomass coincides with 63% of variance in total biomass. Furthermore, nearly all variation in biomass of adults was due to variation in biomass/density of adult males, since biomass/density of adult females was relatively constant ($r^2 > 99\%$ for males, 53% for females; see also McCullough 1981). Means and standard deviations for densities of female and male adults are, respectively, 44.2 ± 2.3 (± 5%) vs. 37.2 ± 11.5 (± 31%). Thus, the percentage standard deviation for density/biomass of adult males was about 6-fold greater than that for adult females.

Note that all variance in estimated biomass of adults of either sex was due to variance in density of them. For, without data on annual variations in mean weights for each age-sex class, the annual biomass value was estimated by multiplying annual density vs. mean weight (biomass) for the age-sex class over the entire 12-year period 1959-70 (Table 4:5). So all correlations vs. densities of adult males and females apply equally well to estimated biomasses of them. By contrast, correlations on biomass of all adults differ somewhat from those vs. density of all adults, because of the equal "weighting" of male and female adults by density, but heavier "weighting" of male adults by biomass.

As can be seen in Tables 8:1 and 8:2, the *pattern* of correlations between parameters of reproduction and recruitment vs. total population biomass are essentially paralleled by those vs. densities and biomasses of adults--whether one considers both sexes together or separately. What differs are mainly magnitudes of the coefficients of correlation and significance, and coefficients of the regression equations. On average, correlations vs. total biomass of the population are about as strong as those vs. total density/biomass of just adults and vs. density/biomasses of adult males. Correlations vs. density of adult females are weaker, in part because density of adult females was much more stable than density of adult males. Lower per capita density dependent impact by adult females might also have been a factor.

It is important to notice, however, that each of the relationships between a parameter of reproduction vs. densities (or biomasses) of adult males and females involves an outlier. During 1960, densities/biomasses of total adults and of adult males peaked at levels otherwise approached only in 1968-1970. Corresponding values for various reproductive parameters were higher than is consistent with the pattern for other years. The outlier is marked in each figure by an open symbol, whereas data from other years are marked with closed symbols (e.g., □ vs. ■). The net impact of this anomaly on 3 reproductive parameters--cub litter size, interbirth interval,

Table 8:2. Cohort sizes and recruitment rates correlated to postnatal or circumnatal biomass or density of Yellowstone grizzlies, 1959-70.*

	Total Density	Total Biomass	Density of Adults[1]			% Male Adults	Adult Biomass
			Total	Males	Females		
YEAR t: N & BM[2]							
Paired cohort size at ages							
0.5 & 1.5 yrs	-0.185	-0.711	-0.786	-0.846	-0.500	-0.885	-0.809
in yr t+1 yrs	0.30	0.007	0.002	0.0005	0.07	0.0002	0.002
1.5 & 2.5 yrs	-0.084	-0.719	-0.792	-0.825	-0.496	-0.833	-0.807
in yr t+2	0.41	0.01	0.003	0.002	0.09	0.002	0.002
3.5 & 4.5 yrs	-0.223	-0.724	-0.817	-0.847	-0.706	-0.864	-0.822
in yr t+4	0.30	0.02	0.007	0.004	0.025	0.003	0.006
CIRCUMNATAL N & BM							
Cohort size at age							
0.5 yr	-0.488	-0.745	-0.714	-0.727	-0.480	-0.727	-0.719
in yr t	0.07	0.004	0.015	0.01	0.10	0.01	0.015
1.5 yr	-0.028	-0.602	-0.686	-0.717	-0.583	-0.696	-0.697
in yr t+1	0.47	0.03	0.01	0.01	0.06	0.01	0.01
2.5 yr	-0.206	-0.902	-0.825	-0.850	-0.756	-0.858	-0.834
in yr t+2	0.30	0.0005	0.003	0.002	0.02	0.002	0.005
5.5 yr	0.474	-0.383	-0.634	-0.658	-0.370	-0.678	-0.643
in yr t+5	0.83	0.23	0.09	0.08	0.24	0.06	0.08
% Recruitment rate between ages							
0.5 - 1.5 yrs	0.429	-0.398	-0.673	-0.701	-0.350	-0.719	-0.685
yrs t to t+1	0.89	0.13	0.02	0.01	0.20	0.01	0.01
0.5 - 2.5 yrs	-0.027	-0.803	-0.861	-0.884	-0.601	-0.889	-0.871
yrs t to t+2	0.47	0.005	0.001	0.001	0.08	0.001	0.001
0.5 - 5.5 yrs	0.549	-0.226	-0.503	-0.532	-0.186	-0.559	-0.578
yrs t to t+5	0.87	0.33	0.15	0.14	0.36	0.12	0.05

* Values given are r and P:1t. (Data from Tables 3:2, 3:6, and 4:5).

[1] Without the anomalous 1967 datum.

[2] N & BM = Density and biomass, in year t or circumnatally, as labeled.

and whelping level--is revealed when their first principal component is regressed against adult male density (Fig. 8:1). The equations for that factor and its relationship to adult male density are, respectively:

$$F_1 = 5.10*(\#C/L)_{t+1} + 2.01*(IBI)_{t+1} + 2.33*\ln(\#L)_t - 26.0$$
$$= 3.34 - 0.0995*(\#AdM)$$

The anomalous point lies 10.5-fold as far from this regression line as the average deviation for the other points. So too, for at least some parameters, the 1967 datum for adult females is anomalously low. If the anomalous datum is omitted in each case, the coefficients of correlation and confidence rise substantially (Table 8:1). For example, adult male density accounts accounts for 44% of the total variance in the reproductive factor, but 95% of the "typical" variance (95% typ)--that remaining after omission of the outlier (Fig. 8:1).

The purpose of omitting outliers is, of course, to avoid masking of a true correlation or distortion of a regression model used to represent the relationships between a parameter of reproduction or recruitment vs. density of adults. By contrast, for purposes of calculating confidence bounds for predictions, an outlier can be omitted only if the anomaly can be identified as the consequence of some other factor whose influence can potentially also be incorporated into the model.

Values of reproductive parameters that were anomalous relative to density of adults during 1960, were not anomolous relative to indices of nutrient-energy balance (see Chapter 5); so the anomaly

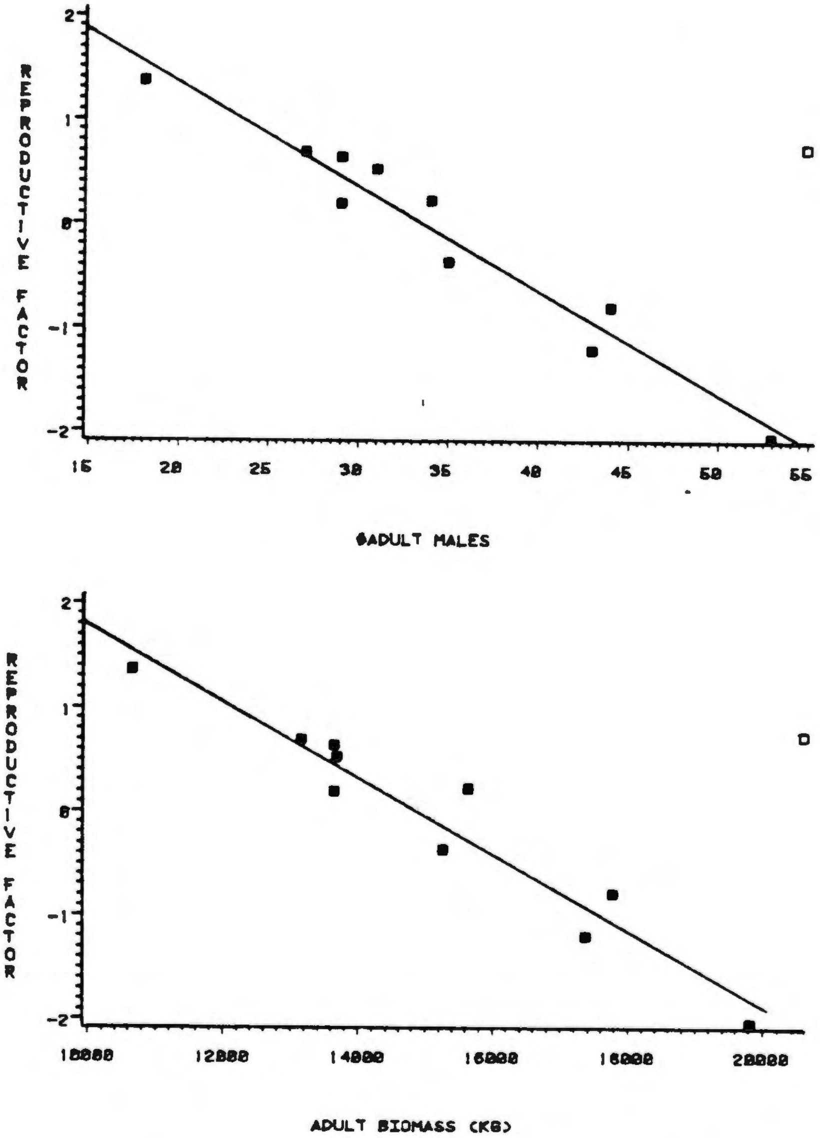

Fig. 8:1. Net effect of adult male density and adult biomass on reproduction, as manifested in the relationships between density or biomass vs. a compound reproductive factor encompassing cub litter size, whelping level, and interbirth interval, at appropriate time lags (see text). (Yellowstone grizzlies, 1959-70). The anomalous 1960 datum is indicated by the open symbol "□" and this and figures Fig. 8:2-Fig. 8:5.

relative to density of adults was presumably due to intervention by variations in food supply or nutrient-energy balance, and perhaps to variations in density and biomass of other age-sex classes. The same applies to the anomalous datum for density of adult females during 1967. Intervening effects of food supply shall be considered again in Chapter 11:II when multivariate models are presented incorporating indices of food supply as well as population biomass or biomasses and densities of adults.

Fig. 8:2 presents plots for cub litter size relative to densities of adult (a) males and (b) females. Note that the predicted change in cub litter size associated with a change from the minimum (40) to maximum (48) densities of adult females is 0.46 C/L. That is comparable to the 0.49 C/L predicted change associated with a rise from the minimum (18) to maximum (55) densities of adult males. If one were to interpret these regression equations as measuring direct causation, one would infer that an increase of 8 adult females reduces mean litter size as much as an increase of 37 adult males--that the density dependent impact per adult female is 4.6-fold as great as the impact per adult male, which seems unrealistic.[1]

Since adult males tend to dominate in competition for food and are larger in body size, one would expect the density-dependent impact

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[1] Actually, these plots represent both density dependent (compensatory, negative feedback) and "density independent" (no feedback) effects on per capita reproductive rate for the population, although the former is most evident. Distinguishing those opposing effects of density shall be discussed in Chapter 13:II.

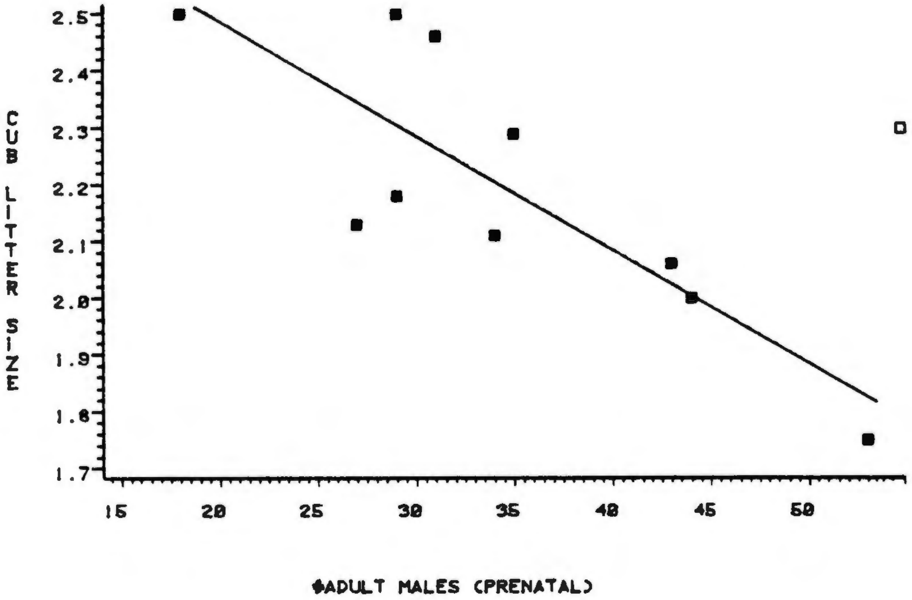

Fig. 8:2. Cub litter size regressed on densities of adult males and females and on adult biomass. Although slopes of these regressions look similar, the difference in scale on the abcissa obscures the fact that the plot regressed on density of adult females is much the steepest--a consequence of correlation rather than direct causation (see text).

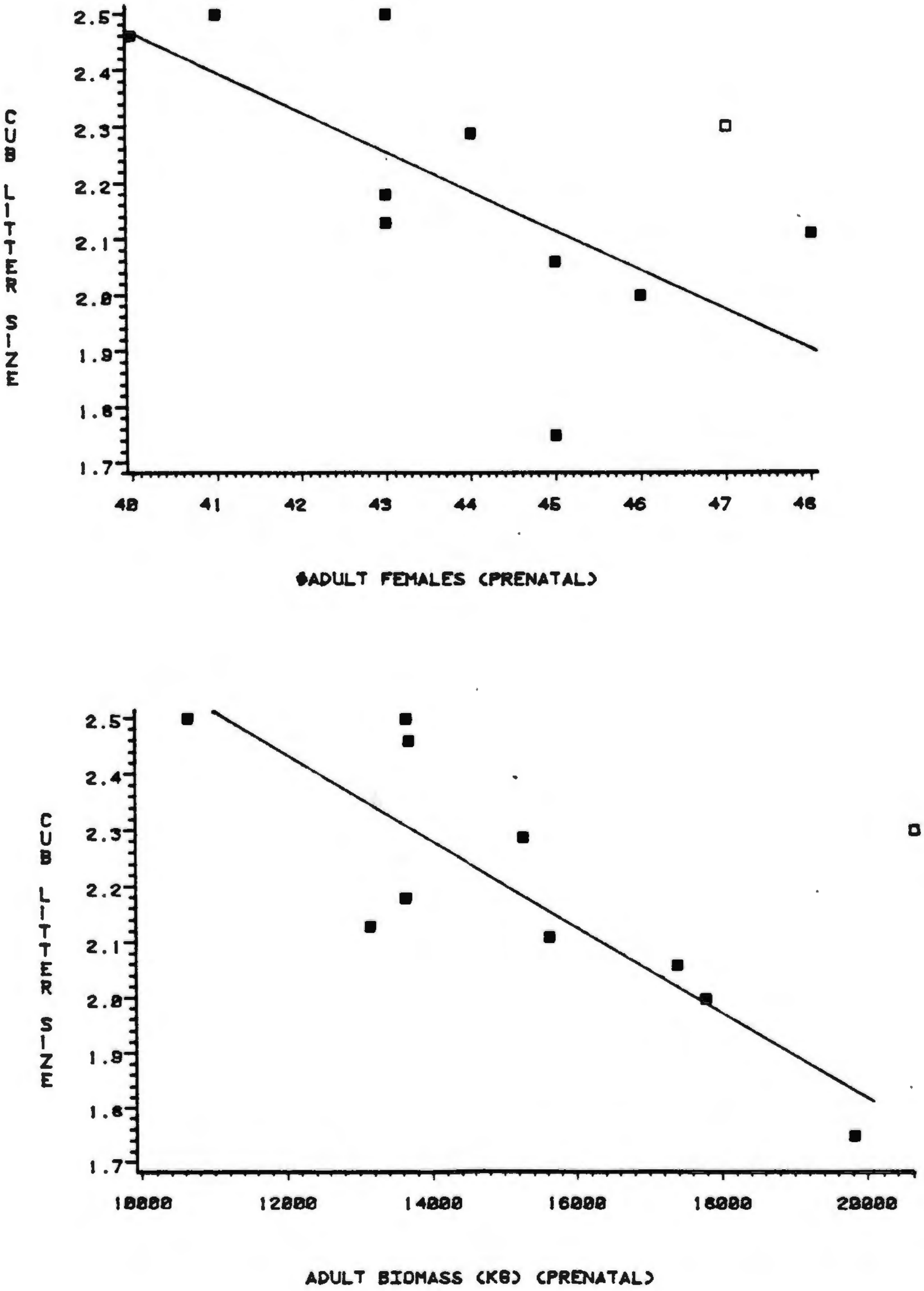

Fig. 8:2. (Continued)

per adult male to be greater, rather than less than that per adult female, probably by a factor at least as great as the difference in their mean body sizes, which is about 1.6-fold in favor of males. What these regression equations really manifest is not direct causal impact, but correlation, the change in cub litter size associated with simultaneous changes in densities of both adult females and males. Indeed, to the extent that cub litter size was reduced by high densities of adults, this control was probably exerted by adults of both sexes, for instance, via food competition. This joint impact was partially obscured by the fact that densities of adult males and females tended to fluctuate together, although magnitude of variation was much greater for males than for females.

If adult males were assumed to have a per capita density dependent impact greater than that of adult females by a factor proportional to their difference in mean body weights (1.6), then their combined causal impact on cub litter size might best be evaluated by regressing cub litter size against total adult biomass. That contrasts to the approach of regressing cub litter size or any other parameter of reproduction or recruitment against total adult density, which tacitly assumes that the impact per adult female is equal to that per adult male (e.g., see Schaffer 1978, 1983; McCullough 1981). The reason that results obtained here for regressions on adult density differed little from those for regressions on adult biomass, can be largely attributed to stability in density/biomass of adult females. Had female density varied as much as male density, regressions on adult density would probably have produced markedly lower correlations than those on adult biomass. This possibility should be investigated with other data.

Regression of cub litter size against total adult biomass (Table 8:2) yields the equation:

$$C/L \;=\; 3.36 - 0.0000769*(BM\text{-}Ad) \qquad r^2=72\% \text{ typ, } P{:}1t<0.001)$$

To convert this to equations for densities of adult males and females, one merely multiplies density of each age-sex class by its mean body weight (adult males 245 Kg; adult females 152 Kg; Table 4:5, p.87).

$$\begin{aligned} C/L \;=\; 3.36 &- 0.0000769*(245)*(\#AdM) \\ &- 0.0000769*(152)*(\#AdF) \end{aligned}$$

Whether or not densities of adults of both sexes are included in the model would, of course, depend upon whether both vary. If subadults and possibly juveniles also exerted density dependent impairment on litter size proportional to mean weight of each age-class, the same procedure could be used to derive a corresponding density dependent term for each of them:

$$\begin{aligned} &- 0.0000769*(130)*(\#3\text{-}\&\text{-}4\text{-yr-olds}) \\ &- 0.0000769*(95)*(\#2\text{-yr-olds}) \\ &- 0.0000769*(65)*(\#\text{Yearlings}) \\ &- 0.0000769*(30)*(\#\text{Cubs}) \end{aligned}$$

Or, if <u>all</u> age-sex classes exert density dependent effects proportional to body weight, then one might instead use the equation obtained by regressing cub litter size directly against total population biomass. However, results presented in Table 8:1 indicate that it was mainly variation in biomass of just adults that exerted density-dependent pressure impairing reproduction and recruitment. So rest of the equations to be given reflect associations with density/biomass of only adult males and females.

Again, the reader is cautioned that the curves given may apply only to the range in adult biomass actually documented. The problem of extrapolation to lower or higher ranges in adult biomass shall be discussed later (Section 8:II.B).

Fig. 8:3 relates density of cubs per adult female vs. adult biomass prenatally. Like the comparable plot for litter size, this appears linear, although its fit is less tight and its slope less steep.

Adult biomass prenatally accounted for 93% of typical variance in the compound reproductive factor (for cub litter size, whelping level, and interbirth interval; Fig. 8:1). So too, adult biomass during the summer of each cohort's conception accounted for 72% of typical variance in just cub litter size. Biomass during the summer of each cohort's infancy--i.e., postnatally--accounted for 47% and 34%, respectively, of typical variance in just whelping rate (#L/AdF) and whelping level (#L) for mothers of that cohort, and 27% of typical variance in the intervals until they whelped again (IBI). (Fig.s 8:4 - 8:6; Table 8:1).

Recall that total density of cubs in each cohort is the mathematical product of litter size and litter density (whelping level)

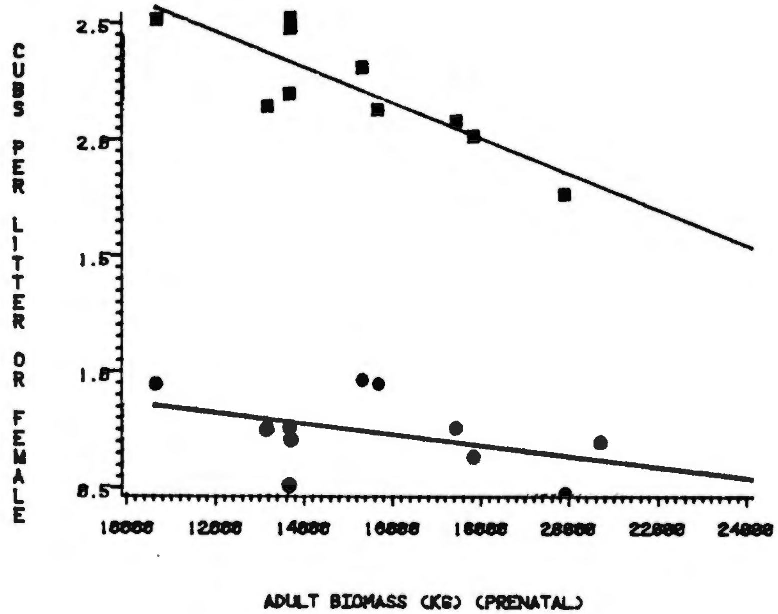

Fig. 8:3. Cub litter size and cubs per adult female regressed on adult biomass prenatally. The lower correlation for cubs per adult female reflects impacts on it by variation in whelping rate which were unrelated to adult biomass. Because whelping rate (#L/AdF) averaged about 33%, mean number of cubs per adult female (#C/AdF) was about 33% as high as litter size (#C/L).

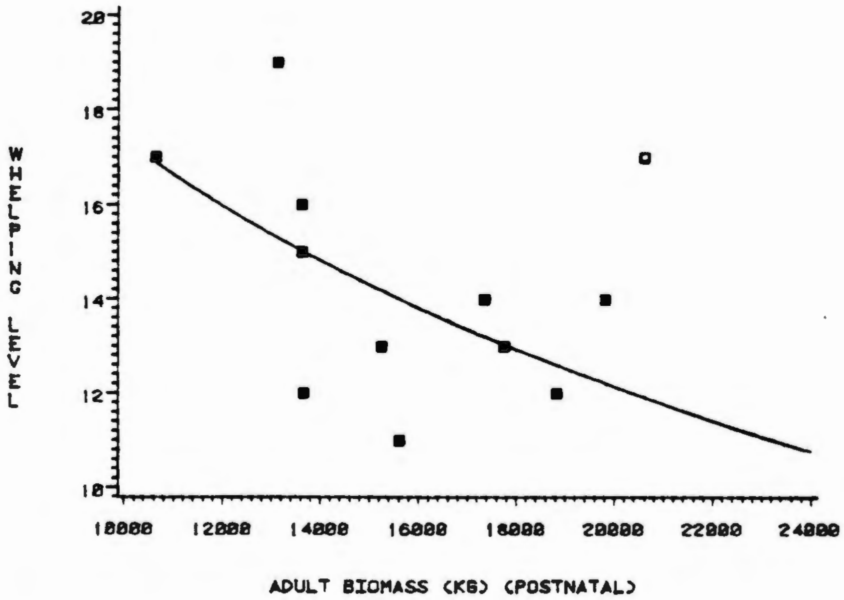

Fig. 8:4. Whelping level regressed on adult biomass postnatally.

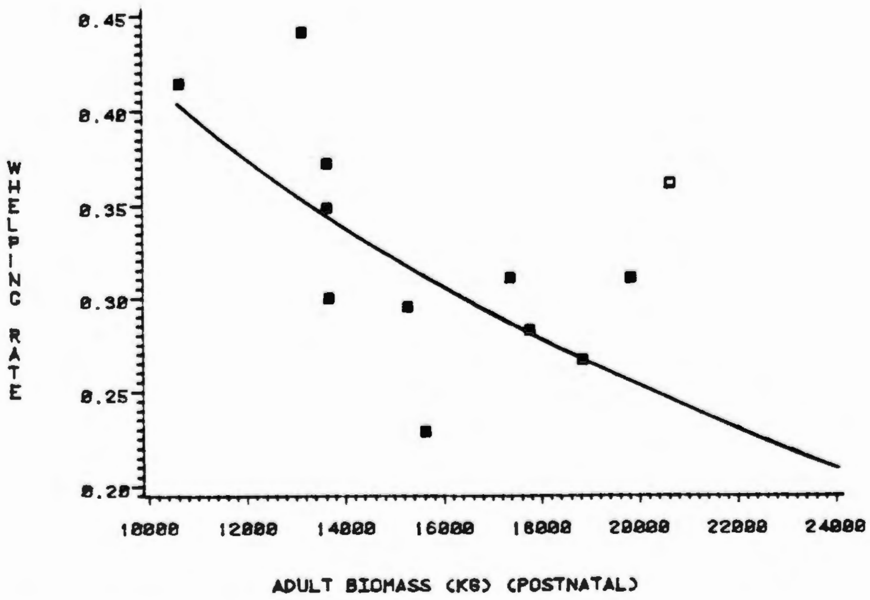

Fig. 8:5. Whelping rate regressed on adult biomass postnatally

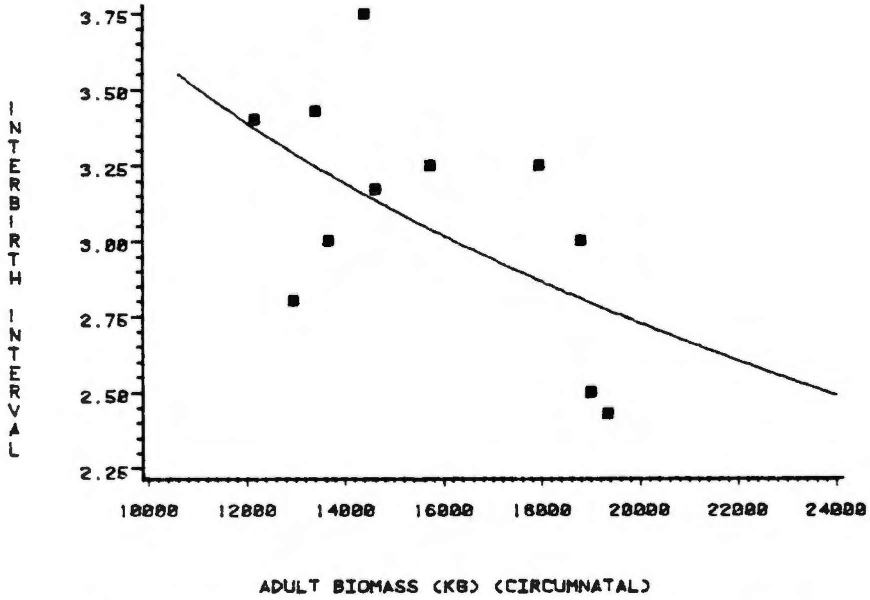

Fig. 8:6. Interbirth interval regressed on adult biomass circumnatally.

$$\#C = \#C/L * \#L$$

Since adult biomass during year t affected density of cub litters born during that same year, as well as mean size of litters born then and during the following year, it affected sizes of both the t and t+1 cohorts. This can be seen by relating adult biomass during year t with combined sizes of each pair of successive cohorts each year at appropriate time-lags, for instance yearlings and cubs during year t+1. The yearlings are members of the t cohort and cubs of the t+1 cohort; year t is when the t cohort was born and the t+1 cohort was conceived. Adult biomass during year t accounts for at least 65% of total variance in combined densities of (a) cubs and yearlings in t+1, (b) yearlings and 2-year-olds in t+2, and (c) 3-&-4-year-olds in t+4 (Fig. 8:7, Table 8:2). Since data on 3-&-4-year-olds were lumped by J. Craighead et al. (1974), combined densities of 2-&-3-year-olds during year t+3 could not be calculated. However, that relationship can be estimated by exploiting knowledge that the 3-yr-olds in t+3 were the 2-yr-olds in t+2, an age when cohort size was known. Combined density of 2-yr-olds in years t+2 and t+3 was also strongly correlated (r^2>70%) with adult biomass in year t (Fig. 8:7).

The results just presented relate adult biomass during each year to combined sizes of the 2 cohorts it affects, at ages 0.5-4.5 years. Another way of viewing these relationships is to consider the long-term response by each individual cohort to adult biomass circumnatally. Cub (0.5-year) litter size is more strongly correlated with biomass prenatally (t-1) than postnatally (t), whereas for

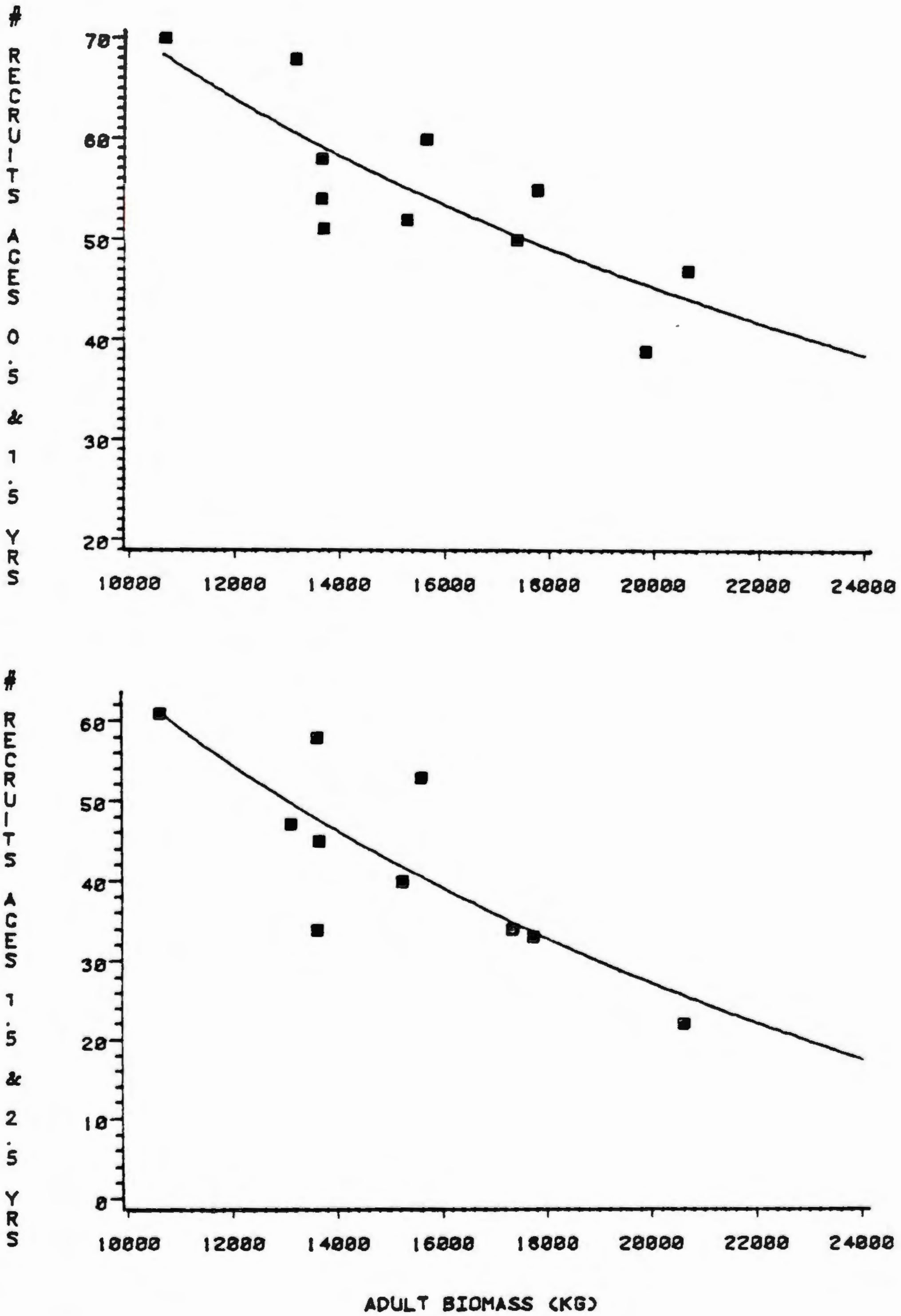

Fig. 8:7. Recruitment to ages 0.5-5.5 for paired cohorts regressed on adult biomass circumnatally (see text).

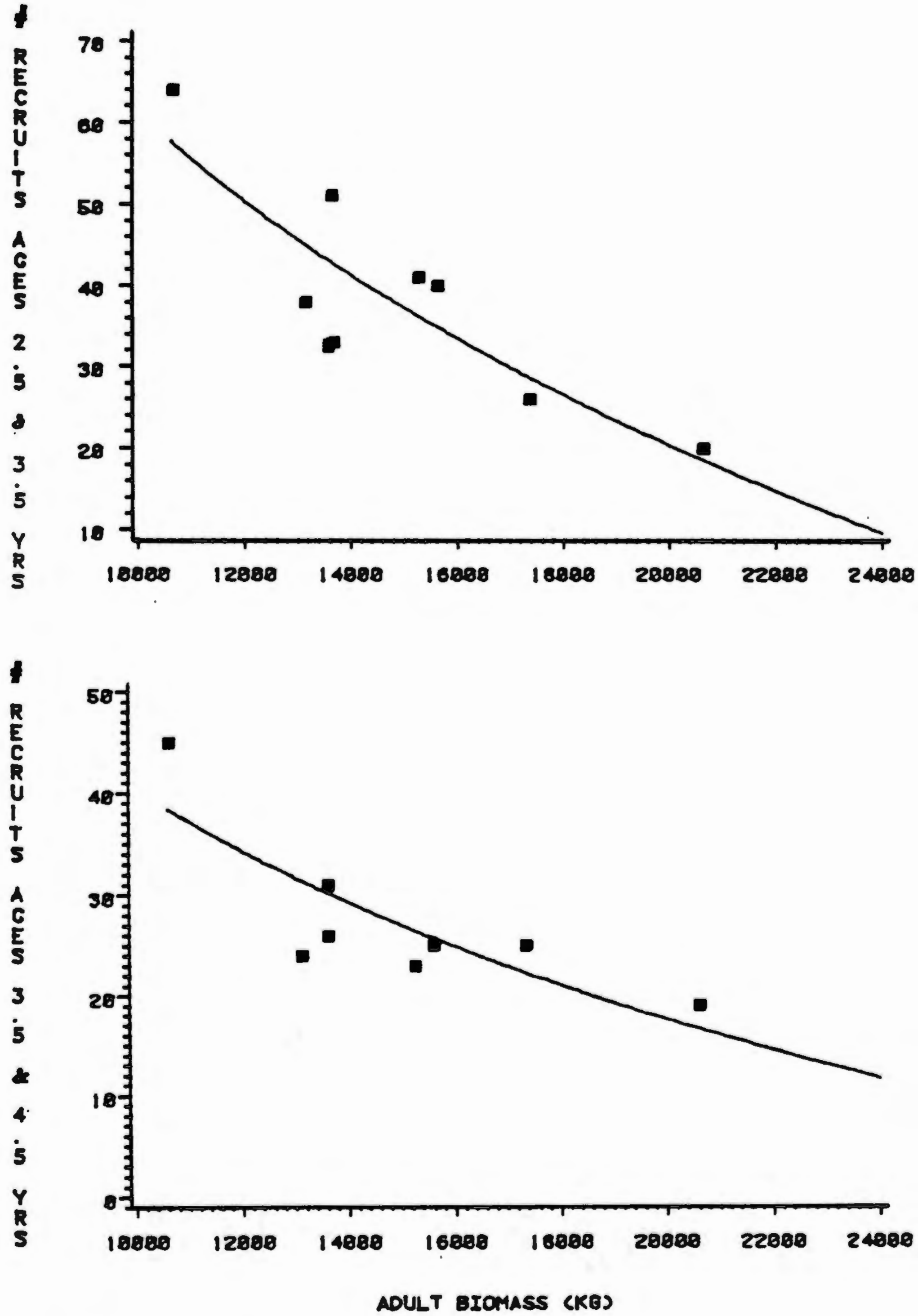

Fig. 8:7. (Continued)

whelping level (#L), just the reverse is true. Thus, size of the t cohort is related to adult biomass during the summers of both its gestation and infancy, i.e., circumnatally.

Adult biomass circumnatally accounts for at least 41% of the typical variance in cohort sizes at ages 0.5 - 2.5 (Fig. 8:8). The correlation is stronger after the 2-year lag (70%) than it was initially, because of the relationships between circumnatal biomass vs. attrition rate between ages 0.5 - 2.5 (76%; Fig. 8:9).~ There is also evidence that adult biomass circumnatally continued to proportionately affect attrition rate at least through ages 3.5, 4.5, and 5.5 years. Granted, data on sizes of individual cohorts at ages 3.5 and 4.5 is lacking. But attrition rate between years t+1 to t+4 for paired cohorts was directly related to adult biomass during year t, when the 4.5-year-olds (t cohort) were born and the 3.5-yr-olds (t+1 cohort) were conceived (r^2=28%). Likewise, attrition rate between ages 0.5-5.5 is positively correlated with adult biomass circumnatally (r^2=33%).[2]

Despite the definite correlations for cohort sizes and attrition rates between ages 0.5-5.5 vs. circumnatal adult biomass, those parameters seem relatively uncorrelated with concurrent adult

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[1] This is in basic, although not specific, agreement with results obtained by McCullough (1981) from regressing cohort sizes at ages 0.5-2.5 vs. density of adults <u>postnatally</u>, assuming parabolic relationships.

[2] McCullough estimated density of 5-yr-olds in a somewhat different way than was done here (Appendix B).

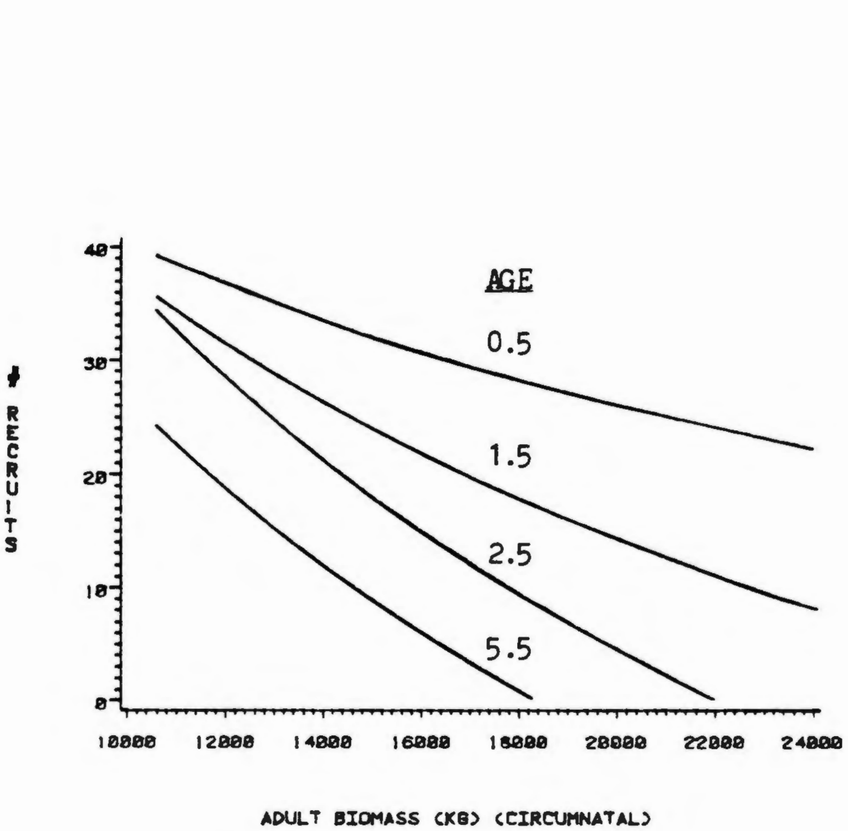

Fig. 8:8. Recruitment to ages 0.5-2.5 and 5.5 years for single cohorts regressed on adult biomass circumnatally (see text).

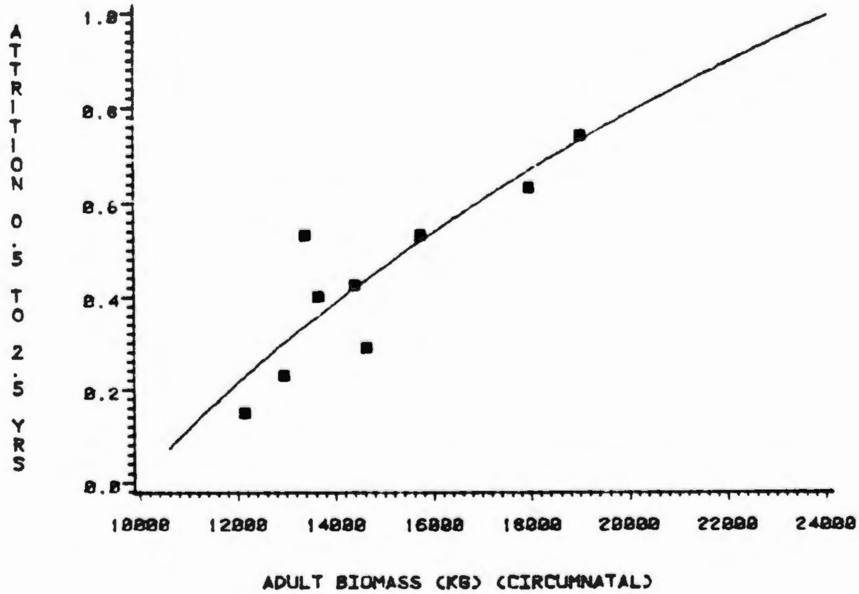

Fig. 8:9. Attrition rate between ages 0.5-2.5 years regressed on adult biomass circumnatally.

biomass and density. The only apparent exception is for cohort size at ages 3.5-4.5 (for adult biomass: r = -0.485, P:1t=0.06). That coincides with expectations that rates of emigration and perhaps mortality, and thus rate of attrition, would increase within 1 to 2 years after offspring were weaned (see Rogers 1977). The fact that interbirth intervals for Yellowstone grizzlies averaged little more than 3 years suggests that most litters were weaned by age 2.5 years. Thus, one might expect dependence on concurrent adult biomass, particularly in terms of adult male abundance, by attrition rate to be higher between ages 2.5-5.5 years than between 0.5-2.5 years, especially for the male immatures.

Because sex ratio was documented for only about 20% of the cubs, on average, McCullough (1981) did not regress cub sex ratio against adult density or sex ratio. Rather, cub sex ratio data was subdivided into 3 groups, each corresponding to 4 years when density of adults was low, intermediate, or high. Results suggested a negative correlation between cub sex ratio vs. density of adults. That was substantiated here by direct regression and Pearson correlations on sex ratio data <u>after</u> estimates had been made for cub sex ratio during years when sample sizes were too small to be usable (Chapter 3:I.D.2). This refinement was necessary in order to (1) quantify the correlation, and to (2) obtain a regression equation that could be used in modeling dynamics of the population.

Circumnatal biomass of adults is also negatively correlated with cub sex ratio (r^2=39% typ), and with density of male cubs (49%

typ), but positively correlated with density of female cubs (9% typ). These figures represent variance remaining after exclusion of just the 1960 datum. If the 1967 datum is also excluded, proportions of remaining variance accounted for by adult biomass circumnatally are 77% (P:1t=0.005), 67% (P:1t=0.01), and 36% (P:1t=0.08), respectively. Thus, when adult biomass was high, few cubs were produced, mainly daughters; when biomass was low, many cubs were produced, mostly sons (Fig. 8:10). (See also McCullough 1981). Whereas the correlation between cub density vs. adult biomass was negative for males, it was appeared slightly positive or for females, if it existed at all. Whereas density of male cubs declined as adult biomass increased (r = -0.701, P:1t=0.02), density of female cubs seems to have increased slightly, if it changed at all (r = 0.298, P:1t=0.22). That might explain, at least in part, why density of female cubs was more stable than densty of male cubs. Means and standard deviations for densities of female and male cubs are, respectively 11.6 ± 3.3 (± 28%) vs. 19.8 ± 7.9 (± 40%). Given that most variation in adult biomass and adult sex ratio was also due to variation in density of males, one finds negative correlations between cub sex ratio vs. density of adult males and vs. adult sex ratio circumnatally (r^2=45%).

As McCullough pointed out, (a) the reciprocal nature of the relationship between densities and sex ratios of cubs vs. adults, and (b) the several-year time-lag between infancy and adulthood, would tend to produce cyclic oscillations in population density and infrastructure at a period of 2 generation lengths. Whether that

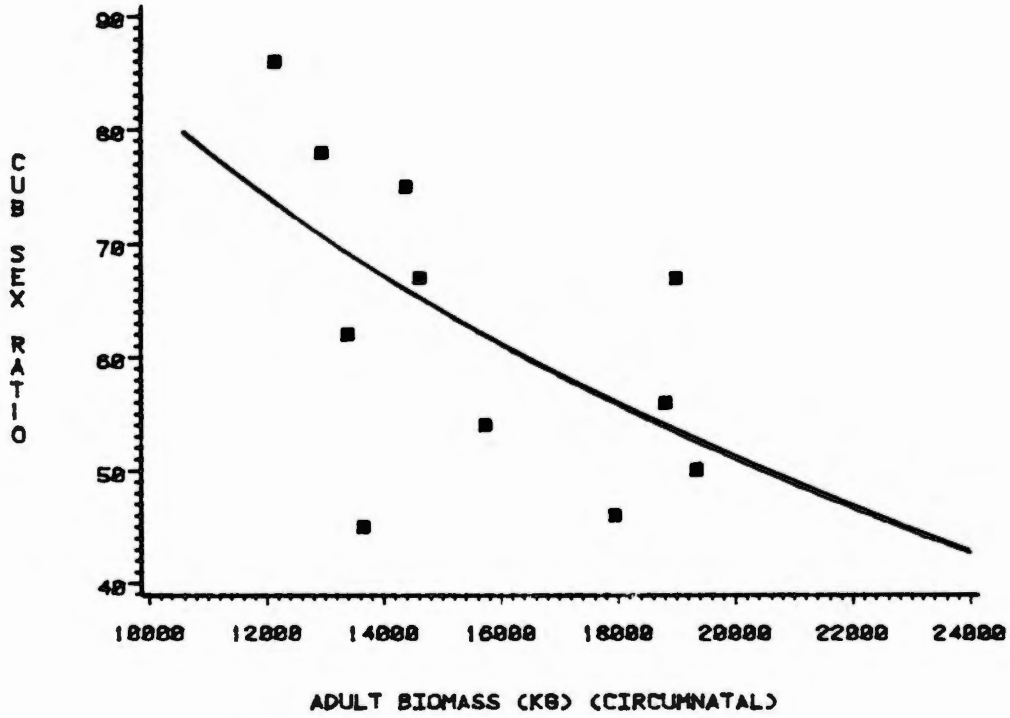

Fig. 8:10. Cub sex ratio (% males) regressed on adult biomass circumnatally.

tendency is actually realized, would depend on relative attrition rates between ages 0.5-5.5 for the different cohorts; according to our results, these would seem to promote oscillations. Occurrence of regular oscillations would also depend on density of older adults (age $\geq$ 6.5 years) when each cohort reaches adulthood. McCullough's prediction seems reasonable, according to both the recruitment models he presented and those presented here. However, simulation tests have to be run to substantiate whether either set of models, much less nature, actually behaves that way. As shown in Fig. 8:11, there is data on density of adult males, as well as cubs, only until 1970. So there is evidence of only 1 supposed cycle. Had density of cubs continued to follow that cyclic pattern after 1970, it would have strengthened the case for cycling per se. But without data on density of adult males during those years, the fact that density of cubs apparently did not continue cycling cannot be used to test McCullough's hypothesis. That lack continued cycling might well be a response to effects of dump closure on both adult male density and, through that and other causal pathways, on cub density.

The nature of the relationships between rates of reproduction and recruitment vs. adult biomass can be further revealed by considering data on each sex separately (Fig. 8:12). Numbers of male and female cubs have already been estimated by multiplying sex ratio for sampled cubs vs. density of all cubs each year (Chapter 3:I.D.2). Densities of male and female 5-yr-olds have also been estimated (Chapter 3:I.D.2., Appendix Tables B:1 and B:2). Curves for ages 1.5

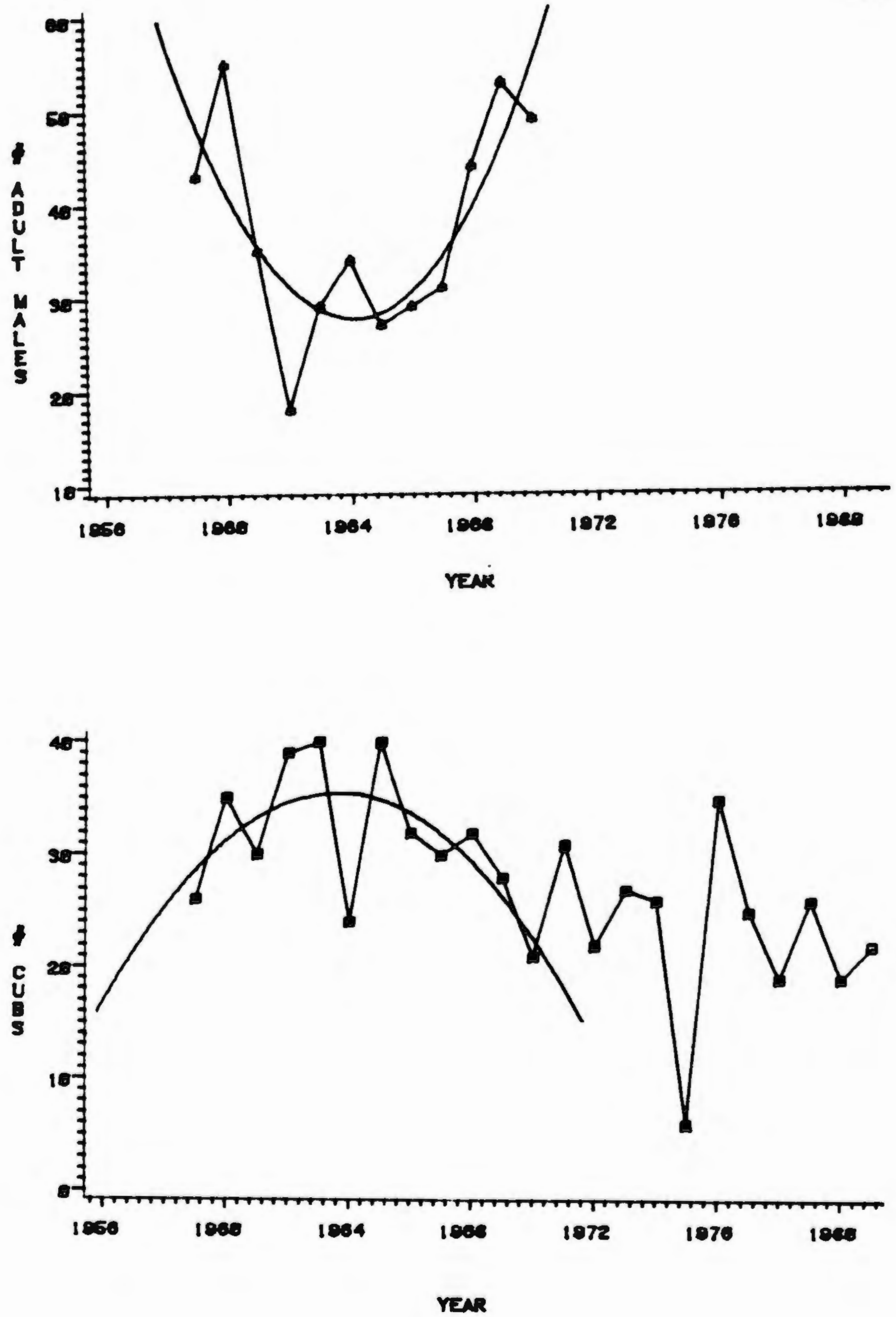

Fig. 8:11. Annual variations in densities of adult males (1959-70) and cubs (1959-81).

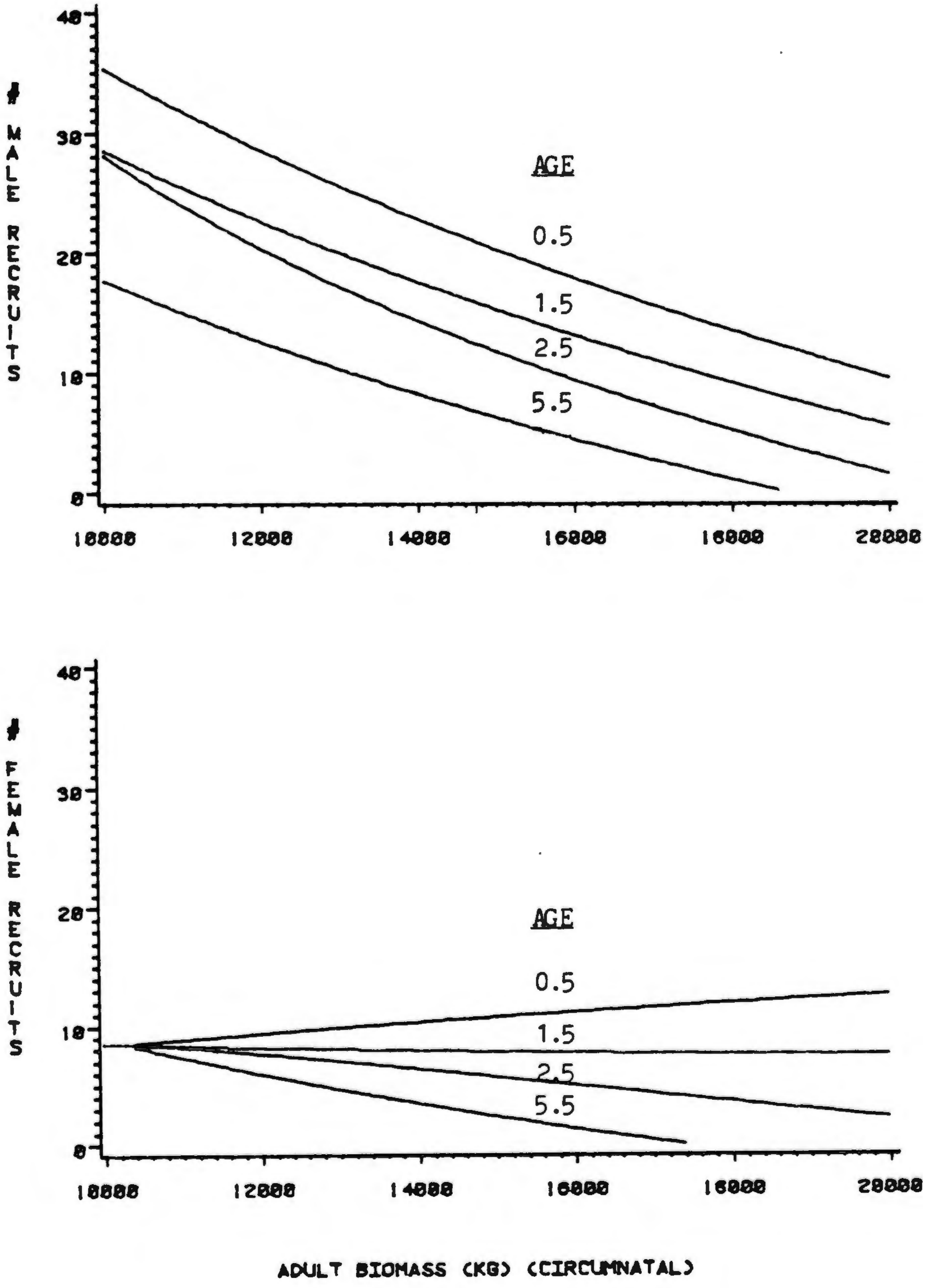

Fig. 8:12. Cohort sizes at ages 0.5-2.5 and 5.5 years for (a) male and (b) female recruits, regressed on adult biomass circumnatally.

and 2.5 were interpolated by the method described in the following section.

8:II.B. Interpolation and Extrapolation

8:II.B.1. Sex Ratios

Estimates for densities of male and female immatures at each intermediate age can be calculated by interpolation based on (a) total cohort sizes, (b) proportion of total attrition between ages 0.5-5.5 that occurred at ages 0.5-1.5, 1.5-2.5, and 2.5-5.5, and (c) total attrition between ages 0.5-5.5 for males and females. For example: At a value of 10,000 Kg adult biomass, predicted densities of recruits of both sexes at ages 0.5, 1.5, and 5.5, are, respectively, 44.2, 37.5, and 26.8. Total attrition between ages 0.5-5.5 is 17.4 (= 44.2-26.8); that between ages 0.5-1.5 is 6.7 (= 44.2-37.5). So, 38.5% (= 6.7/17.4) of the attrition which occurred between ages 0.5-5.5 did so at ages 0.5-1.5. Thus, it is estimated that 38.5% of the attrition for both males and females between ages 0.5-5.5 occurred at ages 0.5-1.5 years. For purposes of this rough estimate, there is not assumed to be any sex differential in the *proportion* of attrition that occurred at any stage of immaturity. Predicted densities of male recruits at ages 0.5 and 5.5 are 35.3 and 17.7, an attrition level of 17.6 immatures; 38.5% of 17.6 is 6.8, giving an estimate of 28.5 (= 35.3 - 6.8) male recruits to age 1.5 in that cohort.

As estimates for densities of cubs and of 5-yr-olds are partitioned by sex, estimation errors are presumably magnified by uncertainties in sex ratios. The separate plots for males and for females have to be interpreted even more cautiously than those for both sexes together (e.g., Fig. 8:12). For instance, the indication of negligible attrition between ages 0.5-5.5 for females at low adult biomass may actually have occurred, by chance; but it is not likely to be typical. Indeed, given the relatively broad confidence bounds for these curves, little faith can be put in the exact slopes attained or thus on the exact levels of attrition they indicate relative to adult biomass circumnatally. The most reliable inferences to be drawn from these curves seem to be the following: (1) Density of cubs produced was affected by rising adult biomass more in the case of males than in the case of females. Whereas cub sex ratio and density of male cubs decreased as adult biomass increased, density of female cubs increased slightly or remained stable. (2) Adult biomass had more impact on percentage attrition rate between ages 0.5-5.5 for males than for females. A change in adult biomass from 10,000 to 20,000 Kg would supposedly increase attrition rate between ages 0.5-5.5 from about 50% to 100% for males, whereas it would increase it from near 0% to 100% for females. On an absolute basis, numbers of immatures lost was greater for males than for females at low adult biomass but about equal at high adult biomass.

8:II.B.2. Cohort Sizes

The range of adult biomasses actually documented, and for which data are available on reproduction and recruitment, was about 10,600 to 20,600 Kg--judging from the data on adult densities and weights presented by J. Craighead et al. (1974, 1980). The regression equations presented so far provide good discriptions of the available data; but how well do they apply at adult biomasses above or below the range documented?

8:II.B.2.a. Adult Biomasses Above the Range Documented

Since every litter must have at least 1 cub, by definition, mean litter size cannot fall below 1.0 C/L. However, if the regression line (Fig. 8:3, p.258) were extrapolated to the abcissa (Fig. 8:13), its X-intercept would occur at 43,629 Kg. By contrast, plots for cubs per adult female (Fig. 8:3, p.258) and total cubs (Fig. 8:8, p.265) intercept the abcissa at 46,581 Kg and 41,443 Kg, respectively. That is good agreement, considering the limited data from which they were derived. But realistically, all should have the same X-intercept, since that is where cub density would supposedly be 0.

The coefficient of correlation for cub litter size is the highest, suggesting that its X-intercept is the most reliable. Equations for the other parameters can be modified to also pass through that point (43,629 Kg) simply by drawing a line from that point through the mean for each of those parameters with respect to the corresponding mean for adult biomass in the case for cubs per

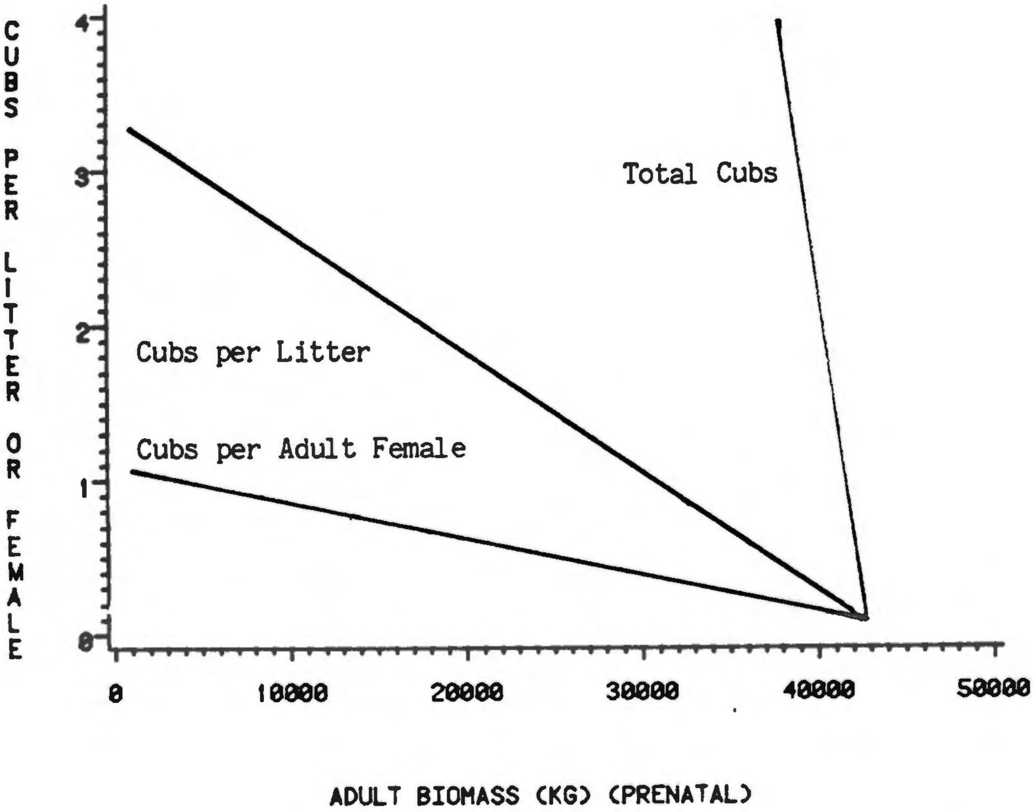

Fig. 8:13. Cub density, cub litter size, and cubs per adult female, regressed on adult biomass. Values were extrapolated above and below the range for which there are data. Slight adjustments of the regression equations for cub density and cubs per adult female were necessary to assure that all have the same X-intercept at high adult biomass, as is logically imperative (see text).

adult female, or through the mean for the natural log of adult biomass in the case of cub densities (i.e., $\bar{X},\bar{Y}$). The point-slope formula yields the Y-intercept. Thus, the equation for the ratio of cubs per adult female is transformed

from #C/AdF = 1.09 - 0.0000234*(BM-Ad)
to about = 1.13 - 0.0000260*(BM-Ad).

Likewise, the equation for cub density is transformed

from #C = 329 - 30.9*ln(BM-Ad)
to about = 315 - 29.5*ln(BM-Ad).

Note that replacement of the original regression lines with these slightly altered lines has too little impact on the coefficient of determination to alter any of the conclusions presented so far (e.g., for #C, r^2 declined just 0.1% from 51.7% to 51.6%).

8:II.B.2.b. Adult Biomasses Below the Range Documented

At adult biomasses below 10,600 Kg, extrapolation of the regression line for cub litter size provides an estimate of 3.35 C/L at a minimum adult biomass of 1 adult male and 1 adult female. Whether mean litter size in the Yellowstone population could ever rise that high, even under the most favorable conditions, is not known. Genetics may limit mean cub litter size to a lower value. The plot for cubs per adult female can also be extrapolated directly.

Whelping rate and level, and thus density of cubs, are also limited, but in a different way. If there were no adults in the population, there could be no litters produced. So each of these curves should pass through (or near) the origin. Thus, each of these curves for cohort size would arise at or near the origin, peak at some moderate level of adult biomass, then decline more-or-less semi-logarithmically towards the abcissa (Fig. 8:14). Thus, they should at least superficially resemble Ricker stock-recruitment models, as shall be discussed in Chapter 13, followed by derivation of an even more appropriate theoretical model.

8:II.B.2.c. Ages for Which Annual Data are Unavailable

Annual data on recruit density for each separate age were provided by J. Craighead et al. (1974) only for ages 0.5-2.5, although density at age 5.5 could be estimated for most years (Appendix B). Those authors lumped data on recruit densities at ages 3.5 and 4.5 and for all adults, although means for each age-class during 1959-67 (prior to dump closure) were given (see Table 8:3). For purposes of modeling dynamics of this population relative to food supply and population biomass/density, one also needs densities for the other ages relative to those factors. Estimation was done in 3 steps:

1) Calculations were made to determine the adult biomasses that would supposedly have yielded the mean densities of recruits (#R, cohort size) at ages 0.5, 1.5, 2.5, and 5.5 reported by J. Craighead et al. (1974: Table 9). For example, 14,645 Kg would supposedly yield 33 cubs, according to the equation:

$$\#C = 315 - 29.5 * \ln(BM\text{-}Ad)$$

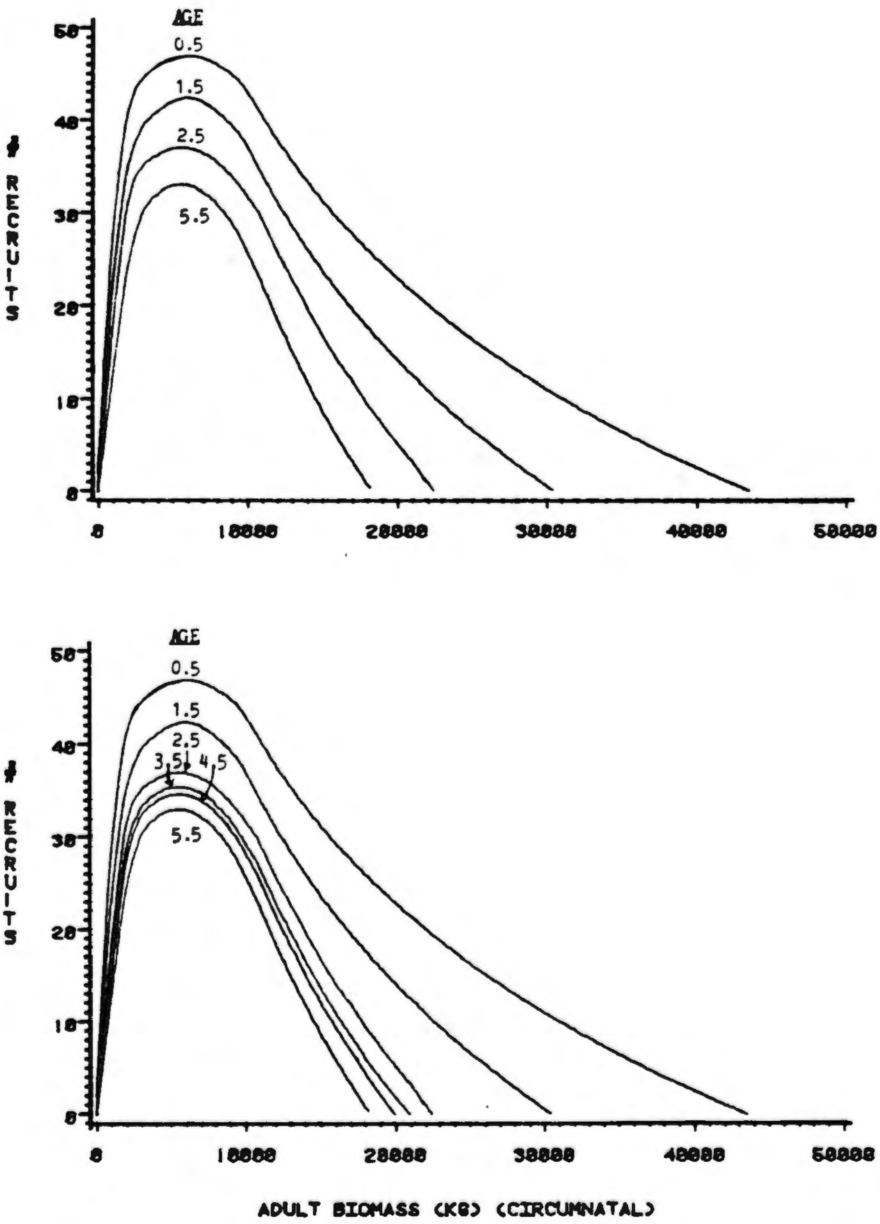

Fig. 8:14. Cohort sizes at ages 0.5-5.5 years regressed on adult biomass circumnatally. Values were extrapolated above and below the range for which data are available. (a) Cohort sizes at ages 0.5-2.5, 5.5. (Compare to Fig. 8:8). (b) Cohort sizes at ages 0.5-5.5, with interpolated values for ages 3.5 and 4.5. The plot for age 0.5 is based on the modification to assure that it has the same X-intercept as cub litter size (see text and Fig. 8:13).

Table 8:3. Infrastructure of the Yellowstone grizzly population for ages 0.5-25.5 years, averaged over 1959-67.*

Age	Number in Age Class			#Recruits[1] Predicted from Adult Biomass	Adult Biomass[2] That Would Predict Observed #Recruits
	Males	Females	Total		
0.5	19.5	13.5	33.0	32.8	14,645
1.5	14.5	8.5	23.0	24.4	15,411
2.5	9.9	8.1	18.0	18.8	15,018
3.5	8.5	5.5	14.0		
4.5	7.0	5.0	12.0		
5.5	3.6	4.1	7.7	9.8	15,428
6.5	3.4	4.0	7.4		
7.5	3.2	3.8	7.0		
8.5	3.1	3.7	6.8		
9.5	3.0	3.6	6.6		
10.5	2.9	3.4	6.3		
11.5	2.8	3.3	6.1		
12.5	2.7	3.1	5.8		
13.5	2.4	2.8	5.2		
14.5	2.1	2.4	4.5		
15.5	1.6	1.9	3.5		
16.5	1.2	1.4	2.6		
17.5	1.0	1.2	2.2		
18.5	0.8	0.9	1.7		
19.5	0.6	0.8	1.4		
20.5	0.5	0.6	1.1		
21.5	0.4	0.4	0.8		
22.5	0.3	0.3	0.6		
23.5	0.2	0.2	0.4		
24.5	0.1	0.1	0.2		
25.5	0.1	0.1	0.2		

* Values from J. Craighead et al. (1974: Table 9).

[1] Number predicted from equations given in text.

[2] Circumnatal biomass which would yield predictions equal to the observed mean densities of recruits aged 0.5-2.5, 5.5 years.

Note how closely these adult biomass values approximate the actual mean value during that period of 14,764 Kg (Table 8:3).

2) Regression through those points yields the equation:

#R = 344 - 0.0214*(BM-Ad) (r = -0.757)

3) Mean density of bears at each of the other ages (3.5-4.5, 6.5-25.5) is marked on that regression line. Those marks are used to determine separation between synthetic curves for estimating how cohort size at each of those ages might have responded to variations in adult biomass.

4) According to those mean values given by J. Craighead et al.: Of the attrition occurring between ages 2.5-5.5, 38.8% occurred at 2.5-3.5, 29.1% at 3.5-4.5, and 41.7% at 4.5-5.5 years. Those percentages are then used at each level of adult biomass to derive the corresponding curves for sizes of those cohorts at those ages (Fig. 8:14). In case the lower attrition rate between ages 3.5-4.5 is an artifact, other ratios (e.g., 43.3%, 33.3%, 23.3%) for ages 2.5-5.5 shall also be assesed in the simulation modeling.

5) At this stage, estimation of how attrition past age 5.5 varies relative to adult biomass circumnatally can be done only by guesswork. Three possible starting points are given below: The correlation between attrition rate among adults vs. adult biomass circumnatally, was a) still positive, b) negative, or c) zero. Examples of scenarios "a" and "b" are given in Fig. 8:15, and disscussed below. Note that past age 5.5, cohort sizes are given only at 5-year intervals. Although these curves are for bears of both sexes, the

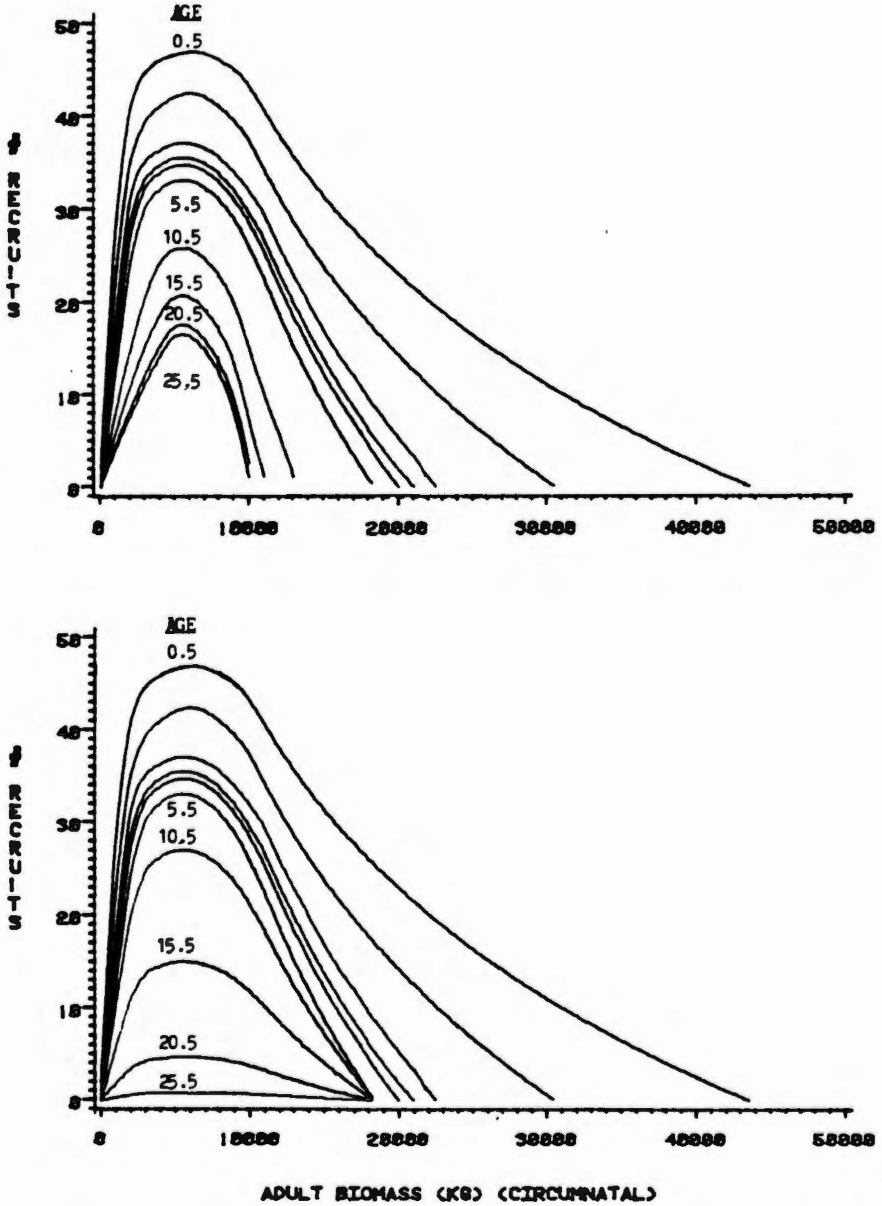

Fig. 8:15. Cohort sizes at ages 0.5-25.5 years, regressed on adult biomass circumnatally. Values were extrapolated above and below the range for which data are available. Curves at ages 10.5-25.5 are given at 5-year intervals, and are entirely schematic. They assume that the correlation between attrition rate vs. adult biomass circumnatally was still (a) positive or (b) negative, to indicate how such reltionships would affect the model.

same method might be used to estimate separate densities of males and females in each cohort at each age relative to adult biomass during gestation and infancy of the cohort.

Scenario A: Suppose that the positive correlation between attrition rate vs. adult biomass circumnatally continued throughout adulthood-- perhaps because adult biomass during gestation and infancy of each cohort permanently affected phenotypic quality of the cohort (Chapter 6:IV.B). Then, the corresponding curves would suggest that, under circumstances better (levels of adult biomass lower) than those occurring in YNP during 1959-67, some bears could potentially live much longer than 25.5 years (Fig. 8:15a). Whether that actually would occur is unknown. The maximum recorded age for both wild and captive bears seems to be about 30 years (e.g., Schoonmaker 1968). Although there are cases of captive polar bears reaching about 40 years (Perry 1966), it is doubtful that this occurs in the wild, due in part to wear and breakage of teeth and claws.

Scenario B: It is possible, of course, that attrition rate did not continue to be positively correlated with circumnatal biomass of adults. Indeed, cohorts which had the lowest rates of attrition as immatures (Fig. 8:15b), perhaps due in part to better phenotypic quality, might have suffered higher rates of attrition as adults. Geist (1971, 1978) reported that for mountain sheep, attributing it to the more "expensive" life style of higher quality cohorts. They expended more energy and took greater risks in play and in various forms of reproductive competition, including combat for mates and investment in offspring--apparently increasing fitness at the expense of longevity.

The possibility of this occurring in bears should be investigated. But even if it does not, cohorts with the largest initial (0.5 year) sizes and lowest rates of attrition to adulthood would recruit the largest number of new adults. So, on average, these recruits would probably encounter more competition as adults than would those from poorer quality cohorts of the same age. This alone might lead to higher rates of attrition among adults in cohorts which had suffered less attrition as immatures. The recruitment curves past age 5.5 might also tend to flatten out if much of the attrition by subadults was due to egress to margins of the Yellowstone Ecosystem, followed years later by ingress of the survivors as adults capable of competing for resources in the core habitat and at dumps.

In population modeling to be done after completion of this dissertation, these and other scenarios for attrition rate among adults shall be tested. However, so few adults remain in each age-class and cohort, compared to cohort sizes at younger ages, that the different scenarios of adult attrition might have little effect on population dynamics. This shall be tested with the model.

8:III. SUMMARY

1) As a result of analyzing the data of Craighead et al. (1974) on Yellowstone grizzlies, Schaffer (1978, 1983) reported negative correlations between cub litter size and whelping rate vs. prenatal

density of adults. On that same data base, McCullough (1981) reported negative correlations between those and other parameters of reproduction and recruitment vs. postnatal density of total adults and male adults. He proposed that negative feedback between densities of cubs vs. adults would produce a cyclic oscillation in age-sex infrastructure of the population.

2) In this chapter, their findings have been extended and elaborated. The statistical approach used here is less subject to serious artifact than the one used by McCullough. Furthermore, whereas McCullough fit logistic-like models to stock-recruitment data, semi-log models were fit here, since they give better fits. Although these semi-log models cannot be directly extrapolated to densities of adults lower than were observed by J. Craighead et al. (1974), they are approximiations of Ricker-like stock-recruitment models appropriate over the whole range of potential densities of adults. Those models shall be presented in Chapter 13.

3) Within the observed range of values, parameters of reproduction and recruitment were strongly negatively correlated with densities of total adults and adult males, as well as with adult sex ratio, but weakly correlated with density of adult females. That difference in strengths of correlations parallels results found earlier by comparison among populations (Chapter 7), for the same reasons: (a) the greater range of variability observed for density of adult males, and (b) the greater per capita density dependent impact by adult males. Because of this difference in per capita impacts by

adult males vs. females, their combined impacts are not best taken into account by simply adding their combined densities (i.e., density of total adults). Rather, their separate densities need to be weighted by a factor corresponding to their per capita impacts; the factor chosen here was mean body weight. Hence, what was added were their biomasses, giving a figure for total adult biomass as a basis for regression and correlation analysis.

4) Cub litter size and the ratio of cubs per adult female were both strongly linearly related to adult biomass. By contrast, other parameters of reproduction and recruitment had strong semi-logarithmic relations with adult biomass.

5) Since most variation in population biomass was due to variation in adult biomass, parameters of reproduction and recruitment were also strongly negatively correlated with total population biomass. By contrast, they were not strongly negatively correlated with total population density, since that was governed primarily by variations in densities of immatures who had little density dependent impact.

6) When adult males were abundant, few cub litters or cubs were produced, mostly daughters. But when adult males were scarce, many cubs litters and cubs were born, mostly sons. Levels and rates of recruitment to adulthood for those cohorts were also negatively correlated with adult biomass circumnatally.

7) Densities of yearlings and 2-year-olds, most of whom had not yet been weaned and dissociated from their mother at the time of

censusing, were not correlated with concurrent density of adult males. By contrast, cohort sizes at ages 3.5-&-4.5 were negatively correlated with concurrent density of adult males. That probably manifests aggression towards the subadults by adult males. This subadult attrition was probably due even more to their egress than to their mortality.

CHAPTER 9

DISCUSSION: PREVIOUS ANALYSES OF THE YELLOWSTONE DATA

9:I. J. AND F. CRAIGHEAD

The Craighead research team has published reports on their demographic data for the Yellowstone grizzlies (e.g., J. Craighead et al. 1969, 1974, 1976, 1980, 1982a; F. Craighead 1979); but little has been presented in terms of analyzing population dynamics (J. Craighead et al. 1973, 1974). The 1974 paper predicted a severe decline in population density due to stresses on the population resulting from closure of the Yellowstone garbage dumps (see Chapter 6:IX). Loss of that food source and increased attrition rate due to human-induced mortality (Table 6:5) were recognized as major stressors; human induced mortality was incorporated into the simulation model. The model regarded density-dependence as negligible and population growth rate as exponential in lieu of evidence to the contrary. However, subsequent analyses by Shaffer (1978, 1983), McCullough (1981), and Stringham (1983) revealed correlations strongly suggestive of negative density dependence for the Yellowstone population.

9:II. F. BUNNELL AND D. TAIT

According to Bunnell & Tait (1981:87),

> Generally, it appears that access to food is not greatly restricted by social factors. Where forage is abundant, populations reproduce well. Dominance hierarchies at concentrated food sources appear to operate primarily in mediating communal access to food by an often solitary and aggressive animal. We

> conclude that reproductive rate is nutritionally regulated in a largely density-independent fashion. (p.87)

Clearly, that disagrees with evidence from comparison among populations and among years for the Yellowstone population, that reproductive rate is negatively density dependent. However, the Yellowstone results are consistent with their conclusion that recruitment rate of immatures (especially male immatures), is strongly dependent on rates of "murder" and eviction by the adult males. Differences in their simulation results obtained on the relatively unhunted Yellowstone population vs. results on a heavily hunted Yukon population are said to substantiate that view.

9:III. D. McCULLOUGH

9:III.A. Fits of Regression Curves to Data

McCullough (1981) fitted parabolic stock-recruitment curves to the origin (0,0) and to data on densities of recruits vs. postnatal densities of adults (total, females, and males). For cohort sizes at ages 0.5, 1.5, and 2.5, vs. density of adult males, the coefficients of determination given by McCullough (Table 1) are 71.4%, 59.8%, and 64.5%. Those coefficients and their confidence levels are so high that one would initially infer that these parabolas give good fits to the data. But, in fact, they do not. The variance they account for so well includes not only variance in the data, based on deviations of data points from the data mean, but also the additional variance inherent in deviation of the origin from the data mean. Because the parabolas are forced through the origin, they account for nearly all variance relative to the origin. Yet, they account for far less of the variance relative to the data itself--5%, 22%, and 41%, for cohort sizes at ages 0.5, 1.5, and 2.5 years, respectively (judging from parabolas obtained here by Y/X vs. X regression). By contrast, the corresponding semi-log models used here (Chapter 8) account for over twice as much of variance in the data itself: 31%, 47%, and 68%, respectively, for cohort sizes at ages 0.5, 1.5, and 2.5 (Fig 9:1).

McCullough was not unaware that his approach could generate such artifacts, so let us consider his justification for using it anyway. To derive those parabolas, McCullough regressed density of recruits at age a (a=0.5 for cubs) in year t+a per adult in year t (postnatally) vs. density of adults in year t. Then, that equation of form

$$\#R/Ad \quad = \quad u \quad - \quad v*(\#Ad)$$

was converted to a parabolic polynomial via multiplication of each term by density of adults:

$$\#R \quad = \quad u*\#Ad \quad - \quad v*(\#Ad)^2$$

As Ricker (1975) pointed out, this procedure yields an unbiased approximation comparable to that obtained by direct regression of #R vs. #Ad. Ricker (p.352) states: With a regression of form Y/X vs. X,

> random variation will tend to generate a negative slope (curved [hyperbolic], it is true), in the absence of any real relationship. However, when a relationship of some consequence does actually exist, the random component adds little to any straight line that is fitted ....

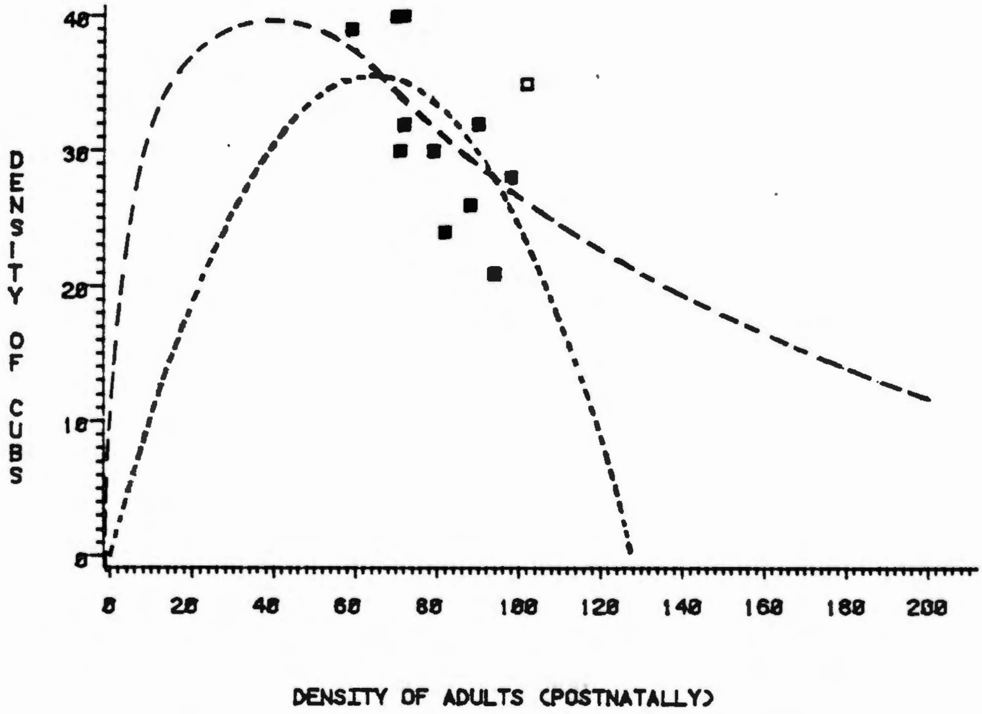

Fig. 9:1. Cohort size for cubs (age 0.5 yr), regressed on density of adults postnatally, for Yellowstone grizzlies (1959-70). Comparison of fits to data obtained using a parabolic model derived by regression of #C/Ad vs. #Ad (after McCullough 1981) as shown with the line of short dashes, versus that using a semi-log model, as shown with the line of long dashes. Interpolation between empirical data and the origin (0,0) for the latter model is schematic. Coefficients of determination for these models are 5% (parabolic) vs. 31% (semi-log) (see text).

Thus, when parabolas are fit not by Y/X vs. X regression, but directly by (a) regression of Y vs. X and by (b) being forced through the origin, similar curves are obtained. The resulting coefficients of determination and confidence level are also similar. But in the case of Yellowstone grizzlies, all of these coefficients are artifacts. For the fact that the origin lies far from the data makes it exert correspondingly greater "leverage" (and violates the assumption that the distribution is normal). Even a straight line run from the origin through the empirical data yeilds a spuriously high coefficient of determination.

9:III.A.1. Variance Reduction

R/Ad vs. Ad autoregression is mainly useful where (1) one does not have access to a computer or to a calculator which can perform polynomial regressions, such that one has to rely on a linear approximation method, or (2) where variance in Y is proportional to X such that variation in Y increases as X increases. (For instance, percentage variation in population size around some trend line might average ±P% [e.g., ±10%], regardless of absolute population size; then absolute magnitude of the variations would be directly related to population size; e.g., see Ricker 1975; McCullough 1979: Fig. 6.6). In Y/X vs. X autoregression, magnitude of variation for Y/X is an inverse function of that for X. The larger X becomes, the smaller the variance in Y/X, relative to variance in Y. Therefore, in some such cases, Y/X vs. X autoregression tends to equalize variance in the dependent variable over the whole range of values for X. Then, as noted above, the line

$$Y/X = u - v*X$$

can be converted into an unbiased estimate of the parabola

$$Y = u*X - v*X^2$$

However, the conventional statistical solution to the problem of regression on data with variance proportional to X is not Y/X vs. X autoregression, but weighted regression. Weighted regression yields tighter confidence bounds around the regression line (Ranney, pers. comm.), and does not bias coefficients of determination or confidence level.

Bias in those coefficients arise if one calculates them for the relationship Y/X vs. X and then applies them to the relationship for Y vs. X--just the opposite of the procedure proposed here (Section 9:III.B below). Not only should these coefficients be calculated directly for the Y vs. X relationship, in order to quantify fit of that curve to the X,Y data, but the coefficients obtained for Y/X vs. X do not necessarily apply even to that relationship.

9:III.A.2. Autocorrelation

If one regresses 1/X vs. X, one obtains a hyperbolic relationship (Fig. 9:2). The plot begins with a Y-intercept at positive infinity, declines rapidly as X increases, and then begins to level off asymptotically towards 0 as X continues increasing towards

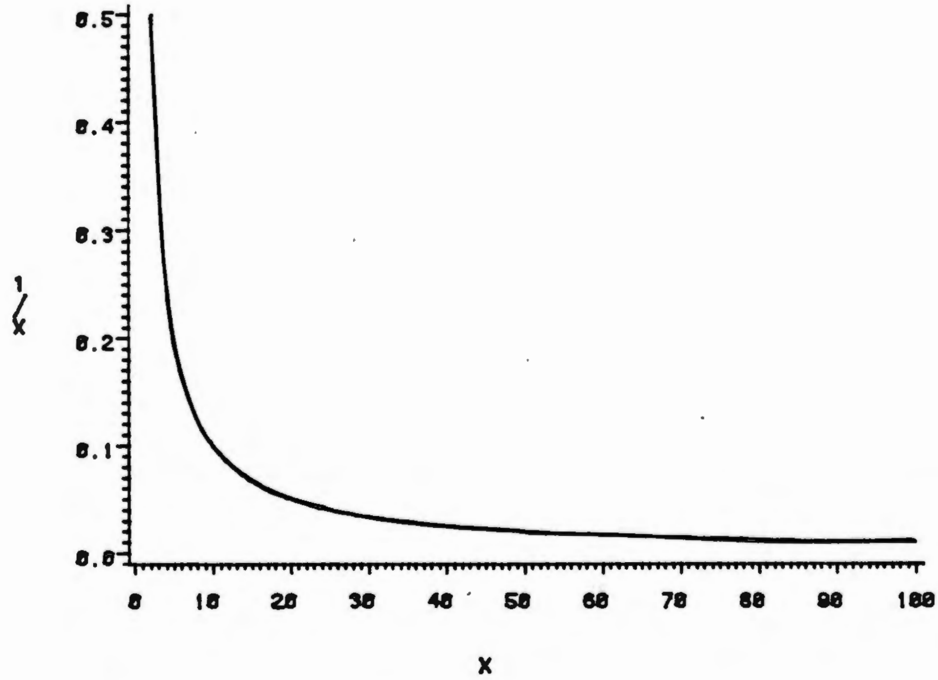

Fig. 9:2. Hyperbolic relationship between a variable and its inverse (X vs. 1/X).

positive infinity. (1) If Y is uncorrelated with X, then a regression of Y/X vs. X also tends to be hyperbolic, but with scatter around the regression line. It is when data are taken (a) from a sufficiently narrow range of values for X (e.g., #Ad), or (b) at high values of X, or (c) when sampling error obscures the hyperbolic shape, that the relationship appears linear. (2) On the other hand, if Y is negatively correlated with X, shape of the hyperbolic curve can be modified somewhat; how strongly it is modified depends in part upon strength of the correlation between Y vs. X and possibly on relative magnitudes of the coefficients of variation (percent standard deviations, %SD) for Y and for X (see below). This hyperbolic tendency is obvious in McCullough's plot (1981: Fig. 5) for the relationship between densities of 3+4-yr-olds$_{t+2}$ per 2-yr-old$_t$ vs. density of 2-yr-olds$_t$. It is also evident in his book (1979: Fig. 6.1) The George Reserve Deer Herd, even though that plot represents 3 supposedly linear relationships, instead of just 1. The hyperbolic relationships are revealed in those particular cases because the plots were presented in the Y/X vs. X form rather than having been transformed into parabolas.

The relationship between Y/X vs. X is thus the resultant of the relationships between Y vs. X and 1/X vs. X. The latter has a correlation of -1.000 for a hyperbolic curve, and generally somewhat less for any linear approximation over a short range of X values. So too, the relationship between Y/Z vs. X/Z is the resultant of the relationships between Y vs. X and Z vs. Z; the latter is linear and has a +1.000 correlation. (Recall that this source of bias was pointed out in Chapter 7:I as a reason for avoiding regressions of density for one age-class against density of another for comparison among populations.) Consequently, whatever the sign and magnitude of the correlation between Y vs. X [$r_{y:x}$], that for Y/X vs. X tends to be more negative and that for Y/Z vs. X/Z to be more positive than $r_{y:x}$.

To elucidate this point, Dr. G. Ranney of the University of Tennessee Statistics Department, developed an algorithm for calculating the correlation between Y/X vs. X (i.e., $r_{y/x:x}$) for any given correlation between Y vs. X and a FORTRAN program for verifying these results by simulation. When these calculations and simulations were carried out, both approaches gave the same results (Ranney & Stringham, in prep).

These results (Fig. 9:3) show that the correlation between Y/X vs. X depends not just on the correlation between Y vs. X, but also on the relative magnitudes of the coefficients of variation, that is the percent standard deviations (%SD = SD/Mean), of Y and X. This can produce highly distorted results. Let us take the simplest case, that where the relationship between Y vs. X is linear, and consider 3 anomalies.

1) If the %SD ratio for Y:X $\geq$ 1:4, then $r_{y/x:x}$ is roughly -1.00, regardless of sign or magnitude of $r_{y:x}$, and even if values for Y and X are chosen completely at random.

2) If $r_{y:x} = 0$, then $r_{y/x:x} = 0$ only if the %SD ratio for

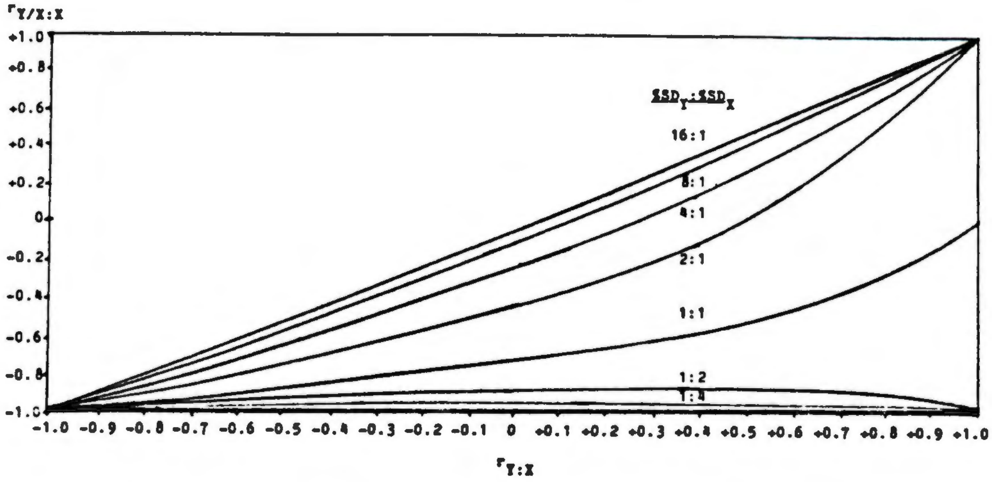

Fig. 9:3. Relationships between correlation coefficients for Y vs. X and Y/X vs. X regressions on the same data, where the relationship between Y vs. X is linear. Whereas the coefficient of determination for a Y vs. X relationship represents the amount of information about Y provided by X, the coefficient for a Y/X vs. X relationship cannot be interpreted in that same way, because of effects on the coefficient by the ratio of percent standard deviations for Y and X (see text).

Y:X > 16:1. If the %SD ratio is about 1:1, $r_{y/x:x}$ is about -0.70.

3) If $r_{y:x} = +1.00$, then $r_{y/x:x}$ has a value of either +1.00, 0.00, or -1.00, depending only upon whether $\%SD_y$ is, respectively, greater than, equal to, or less than $\%SD_x$, regardless of how small the imbalance is. For example, results calculated for an imbalance of only 0.001 are given in Table 9:1. Clearly, these distorted correlation coefficients can be misleading both in terms of sign (+ or -) and magnitude of correlation.

Those distorted coefficients can also imply that one has much more information about Y/X than is actually the case. For they reflect not only the information provided about Y by X, but also the information embodied in X about itself. Suppose that $r_{y:x} = 0.20$ and the %SD ratio is 1:1; then $r_{y/x:x}$ would be roughly -0.60 or, if %SD ratio is 1:4, $r_{y/x:x}$ would be almost -1.00. Clearly, this difference in magnitudes of correlations (-0.60 vs. -1.00) cannot be understood in terms of any difference in amounts of information provided about Y/X by X. (Relative and absolute magnitudes of %SD for a factor indicate how varible it is, not amount of "noise" or uncertainty in the data.)

With these facts in mind, one cannot agree with McCullough's statement that:

> If there were no compensatory mechanism in the population, then the number of young recruited (R) to a given juvenile age and the recruitment rate (R/N) should be independent of the size of the adult population (N) producing the recruits. Thus, a regression of R/N on N should produce a more-or-less random scatter of points with a slope not significantly different from zero.

Table 9:1. Major changes in the correlation between *Y/X vs. X* as a function of miniscule changes in the ratio of percent standard deviations for Y vs. X.

Ratio of %SD Y : X	$r_{y/x:x}$[1]
1.001 : 1.000	+1.000
1.000 : 1.000	0.000
0.999 : 1.000	-1.000

[1] These results demonstrate the fact that the coefficient of correlation for *Y/X vs. X* does not necessarily correspond to the amount of information X provides about Y/X (see text).

Instead, the test of significance might be based on whether the slope obtained for R/N vs. N differs from the strongly negative (e.g., hyperbolic) slope produced if R is randomly related to N. Or, autocorrelative regression might be avoided entirely, as discussed below.

9:III.B. Avoiding Autocorrelative Biases

In many cases, the best way of avoiding the dilemma of appearing to have more information than one actually does, and of calculating reliable coefficients of correlation, determination, and regression, seems to be use of the procedure proposed by Ranney (pers. comm).

(1) Regress Y vs. X; to obtain the equation
$\hat{Y} = f(X)$ and thus the estimated $\hat{Y}_i$ for each X_i.

(2) Divide each $\hat{Y}_i$ by X_i.

(3) Plot $\hat{Y}_i/X_i$ vs. X_i (rather than the curve found by regressing $[Y/X]_i$ vs. X_i.

The coefficients of determination and confidence applicable to the curve $\hat{Y}_i/X_i$ vs. X_i are those calculated originally for Y vs. X, because these subsequent calculations just transpose the original information from one form to another without adding any further noise or information--despite revealing new insights. (Relationships of form Y/Z vs. X/Z can be handled comparably). An example of this method would be to take the semi-log curve obtained here for density of cubs vs. density of adults:

#C = [315 - 29.5*ln(BM-Ad)] (r^2 = 52%, P:1t=0.015)

Division of each term by BM-Ad yields

#C/Ad = [315 - 29.5*ln(BM-Ad)]/#Ad (r^2 = 52%, P:1t=0.015)

Ranney's procedure seems to make perfect sense in cases where Y is not intrinsically related to X, as when one regresses

#C/#Ad vs. #Ad

But question remains about its applicability to a relationship such as

#C/L vs. #L

in cases where every cub counted is a member of one of the litters (as was the case for the YNP data). To follow Dr. Ranney's procedure would involve regressing

#C vs. #L

= (#C/L)*(#L) vs. #L

a regression of form <u>Y/X*X vs. X</u>, which also involves autocorrelation. Only if #C/L and #L were counted independently of one another, would autocorrelation be avoided.

The same problem arises in trying to assess how sex ratio (percent males, %M) for any maturity-class varies relative to total size of that class. For example, with cubs:

%MC vs. #C

= #MC/#C vs. #C

(Where #C = #MC + #FC; MC = male cubs, FC = female cubs).

Indeed, the problem of autocorrelative regression is common in population analysis and may be unavoidable in some cases. If used, care should be taken to estimate how seriously that could bias results, as was done here.

Recapitulating: The parabolic curves presented by McCullough (1981) for recruit densities at ages 0.5, 1.5, and 2.5, relative to postnatal density of adults, fit the data only half as well as the semi-log curves presented here, despite the fact that the coefficients of determination for the parabolas, based on those for relationships of form #R/Ad vs. #R were often higher. Those higher coefficients are artifacts of autocorrelation. While these and other autocorrelative biases seem to distort many of the quantitative results obtained by McCullough (1979, 1981), they do little to alter most of his qualitative conclusions, judging from similarities in the findings obtained here. Thus, these results (a) refine those by McCullough, as well as (b) extend them to additional variables, ranges of values for the variables, time-lags, and ages, and (c) prepare the way for integrating responses by parameters of reproduction and recruitment to density/biomass with responses to food supply (Chapter 11).

9:IV. SUMMARY

1) McCullough's (1981) tests for density dependence in the Yellowstone data were based on autocorrelative regressions. Autoregression is highly controversial because of the artifacts it can generate, for instance gross exaggeration of coefficients for correlation, determination, and confidence level. Although McCullough

argues that such artifacts are negligible in his results, our tests made via basic statistical theory and simulation modeling indicate that his usage of autocorrelative regression is prone to serious bias (Ranney & Stringham, in prep.). That was confirmed for specific examples presented by McCullough, for instance in the regression of cub density vs. adult density postnatally.

2) While autocorrelative regression could not be entirely avoided in this monograph, it was avoided for key relationships which form the core of the differences in results between McCullough's findings versus those presented here on density dependence among Yellowstone grizzlies. Few of McCullough's qualitative conclusions were altered by those differences; but the quantitative models and hence predictions differ substantially.

CHAPTER 10

DISCUSSION: IS EVIDENCE OF DENSITY DEPENDENCE SPURIOUS?

Even in lieu of density dependence, there are several ways in which behavior of bears, relative to one another or to their environment, could produce negative correlations between parameters of reproduction or recruitment vs. density of the population or of adults, especially males. These are artifacts not detectable by significance tests. So observed negative correlations should be further considered accordingly in terms of the null hypothesis that they are spurious, before being interpreted in terms of density dependence.

The fact that, for Yellowstone grizzlies, virtually all parameters of reproduction and recruitment are negatively correlated with density and biomass, particularly density and biomass for adults, has been interpreted as evidence of negative density dependence by Shaffer (1978, 1983), McCullough (1981), and Stringham (1983; Chapter 8). However, J. Craighead interprets those correlations as a spurious consequence of other factors, including food supply, which along with human intervention supposedly did control dynamics of that population (J. Craighead et al. 1982, pers. comm.). Unfortunately, the reasons for this objection have not been stated, nor has J. Craighead offered an alternative explanation on that basis--although some alternatives have been suggested by other critics in response to earlier presentations of my findings (e.g., Stringham 1980, 1983) and those of McCullough (1981), or are obvious. Of particular interest are hypotheses concerning how behavioral differences between age-sex classes might have biased censuses in a way that would give a false impression of negative density dependence. That topic shall be dealt with in 2 parts: (A) Differences in usage of concentrated food sources by each age-sex class. (B) Possible effects of food supply on distribution and foraging behavior by the YNP grizzlies.

10:I. ADULT MALE AVOIDANCE HYPOTHESIS

Dams with cubs commonly avoid feeding aggregation sites and other areas frequented by adult males (*grizzlies*: Stonorov & Stokes 1972; Pearson 1975; Egbert & Stokes 1976; *black bears*: Erickson 1965; Barnes & Bray 1967; Jonkel & Cowan 1971; Lindzey & Meslow 1977b; *polar bears*: Taylor et al., in press). That has led some critics to hypothesize that the negative correlations between densities of cub litters and cubs or older immatures vs. density of adult males at YNP is just an artifact of conducting censuses at dumps. (This supposes, of course, that mean density of adult males at dumps varied directly with their mean density in the population; so far, I haven't the information needed to test this assumption). Granted, dams with cubs might have avoided the dumps when/where adult males were most abundant. However, there are several reasons for doubting that this could account for the statistical indications of negative density dependence.

1) Censuses were also conducted in the backcountry, far from dumps, over a period of several months each year (Chapter 12:I.A). Numerous bears seen at dumps were also seen there.

2) There was considerable variation over the course of each day and from day to day in which bears were at the dumps. If some females with cubs did avoid dumps when adult males were present, they might still have had opportunity to visit dumps at other times. That is the pattern found at McNeil River fishing sites (Stonorov & Stokes 1972; Bledsoe 1975; Egbert & Luque 1975; Egbert & Stokes 1976; see also Frame 1974).

3) A high proportion of the population was individually identifiable over a period of at least several years. Demographic data were collected each year. Despite large annual fluctuation in number and proportion of the adult females producing litters, there was little fluctuation in total number of adult females censused. Reproductive histories of many were documented over the course of up to 3 litters (see J. Craighead et al. 1969, 1974, 1976). So offspring missed as cubs would likely have been censused latter, in following years, and then added to the original count. Dams with older litters are much less likely to avoid food concentrations frequented by conspecifics.

4) Cohorts which were smallest during infancy (i.e., fewest cubs) tended to have correspondingly higher rates of attrition during immaturity, in direct proportion to *circumnatal* density and biomass of adults, particularly adult males.

5) The capacity to individually identify a large number of bears and to radio-track several females with cubs, should have revealed whether such females avoided dumps, exposing this possible source of bias early enough that countermeasures could have been taken in censusing.

6) Cohort size and especially litter size (at age 0.5 year) were correlated with prenatal as well as postnatal density of adult males. In fact, the prenatal correlation was stronger in the case of litter size. This cannot be explained by the adult male avoidance hypothesis.

Thus, even if dam-cub families and subadults tended to avoid dumps when adult males were most abundant there, that is unlikely to have biased censuses enough to account for the negative correlations between rates of reproduction and of recruitment to at least age 5.5 years vs. circumnatal density and biomass of adults.

10:II. DISTRIBUTION AND DENSITY OF BEARS RELATIVE TO FOOD SUPPLY

The question of whether the apparent density dependence in dynamics of the Yellowstone grizzly was really spurious now hinges on 2 other points: (1) Are the correlations found by Shaffer (1978, 1983), McCullough (1981), and myself, as well as simulation results by Bunnell & Tait (1981), evidence of direct causation or merely of association? If merely association, what other causal variables could have controlled both (a) rates of reproduction and recruitment, and (b) density/biomass of adults? (2) Even if density dependence occurred, how much impact did it have relative to impact by food supply and other causal factors?

Answers to these questions shall be approached in 2 steps: (1) Corresponding data on Minnesota black bears shall be reviewed. It is the most thorough information available which is comparable to that on Yellowstone grizzlies, and it does show some similarities to the Yellowstone data. (2) Negative correlations between parameters of reproduction and recruitment vs. density/biomass of adults in that Minnesota population seem spurious, in the sense that both sets of variables seem to have been controlled by food supply. Once that information has been reviewed, its implications for interpreting data on Yellowstone grizzlies shall be considered.

10:II.A. Minnesota Black Bears

10:II.A.1. Results

Recall that for Yellowstone grizzlies, predictions were verified that parameters of reproduction and recruitment were positively correlated with food supply indices, but negatively correlated with density and biomass. Correlations with density of adult females tended to be weaker than those with density of adult males and adult sex ratio. That weakness is attributed to at least 3 factors (Chapter 7:II.A.1.a): (a) greater stability in density of adult females; (b) less negative density dependent impact per adult female; and (c) greater density independent impact per adult female. Correlations between parameters of reproduction and recruitment vs.

population density and biomass also tended to be weaker than those vs. density of adult males. Those same characteristics also typify relationships for Minnesota black bears, despite the fact that no correlation for that population is based on more than 8 years of data and some only on 4 or 5 years worth. However, the pattern of correlations and time lags were not all the same between these 2 populations. Let us consider the similarities first.

Similarities with Yellowstone Grizzlies: Among Minnesota black bears, whelping rate and level were negatively correlated with prenatal densities of adult males ($r = -0.704, -0.693$, P:1t<0.10, n=4) and adult females ($r = -0.400, -0.433$, P:1t<0.25, n=4). Likewise, cub survival rate was negatively correlated with concurrent (postnatal) densities of adult males ($r = -0.911$, P:1t<0.02, n=5) and females ($r = -0.934$, P:1t=0.01, n=5). Although cub sex ratio was correlated with adult sex ratio or density of adult males, it may have been negatively correlated with prenatal density of adult females ($r = -0.659$, P:1t=0.17, n=4), as well as with circumnatal population density and possibly biomass ($r = -0.750, -0.559$, P:1t<0.22, n=4). [1]

Among Yellowstone grizzlies, densities of yearlings and older juveniles showed strong correlations with circumnatal biomass or

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[1] Hesitation is expressed concerning correlations with population biomass because of the fact that biomasses could be estimated only crudely. Data on weights of each age-sex class were not available; so the estimate was made by assuming that the ratio of weights for each age-sex class was comparable to that for Yellowstone grizzlies. When more appropriate weight data become available, the correlations can be recalculated.

densities of adults, but negligible correlation with their concurrent biomass or density. By contrast, density of subadults was negatively correlated with concurrent density of adult males. Among Minnesota black bears, which usually dissociated from their dam and thus became subadults at age 1.5 years, data are available over too few years to support comparable time-lag analysis. But densities of 2- and 3-yr-old subadults were negatively correlated with densities of adults concurrently and during the preceeding year (e.g., $r = -0.879$, P:1t=0.06, n=9, for density of 2-yr-olds vs. density of adult males averaged for years t and t-1).

Differences From Yellowstone grizzlies: Aside from those similarities between the Yellowstone vs. Minnesota results, there were also numerous differences:

1) Although the correlations in whelping rate and level, cub sex ratio, and cub survivorship vs. density or biomass are negative for both populations, for the time lag given (pre-, post-, or circumnatal), some of the corresponding correlations for Minnesota black bears at slightly different time lags are positive, contrary to predictions.

2) Even though cub survivorship was strongly negatively correlated with postnatal density of adult females, it was positively correlated with their prenatal density ($r = 0.524$). Whether that is an artifact of the small sample size cannot yet be determined.

4) Whereas these relationships seem semi-logarithmic for Yellowstone grizzlies, they seem more nearly linear for Minnesota

black bears--another difference which could be an artifact of the small sample size from Minnesota (see Fig. 4:1).

5) Among Yellowstone grizzlies, in agreement with the hypotheses, cub density and litter size were strongly negatively correlated with population biomass and with densities of adults pre-, post-, and circumnatally. Yet, among Minnesota black bears, contrary to hypotheses, cub density and litter size are positively correlated with density and biomass at all of those time lags (e.g., r = 0.854, P:1t=0.03 for cub density vs. adult male density postnatally; r = 0.771, P:1t=0.11 for cub litter size vs. density of adult males prenatally).

Recapitulating: In accordance with predictions, results for Yellowstone grizzlies revealed consistent positive correlations with the food supply index and consistent negative correlations with density and biomass--for the total population and especially for adults. By contrast, results for Minnesota black bears were inconsistent. As predicted, whelping level and rate and cub survivorship among Minnesota black bears were positively correlated with food supply and negatively correlated with adult density. But for cub density and litter size, the reverse is true; that is, where a positive correlation was predicted, a negative one was found, and vice versa.

Granted, for Minnesota black bears, it may be that the correlations for cub density and litter size are only superficially contradictory to these hypotheses. The predicted correlations might have actually existed, but been masked by intervening factors such as effects of maternal age or parity on cub litter size. However, until confirmatory data for such suspicions becomes available, a reviewer can only question whether any of the correlations between parameters of reproduction or survivorship vs. either food supply or density are reliable, either biologically or statistically. Sample size, both in terms of number of bears sampled per year and number of years sampled, is the strongest basis for placing more faith in (a) results concerning whelping level and rate and cub survivorship, which agree with the hypotheses (n=8 yrs), than in (b) the contradictory results concerning cub density and litter size (n=5 yrs).

10:II.A.2. Interpretation

Supposing then that among Minnesota black bears, (1) whelping level and rate and (2) cub survivorship rate, really were positively correlated with food supply, but negatively correlated with density of adults: What is the basis of those latter correlations? For example, to what extent did variations in total population density and in density of adults affect the amount of food obtained per bear?

Causation vs. Association: It is important to note that for the Minnesota bears, adult density was negatively correlated with concurrent food supply (adult males: r = -0.807, P:2t=0.10; adult females: r = -0.646, P:2t=0.24; adult sex ratio: r = -0.890, P:2t=0.04). Limited evidence indicates that amount of travel and probably home range size for black bears tend to increase during periods when local food supplies are inadequate. That was obvious seasonally and perhaps annually for the Minnesota black bears (Rogers 1977, pers. comm; see also Beeman & Pelton 1980). Among Minnesota black bears, one would expect these changes to have been greater for adult males than for adult females, since the males (a) were not territorial, (b) normally had home ranges several fold larger than females, and (c) were more opportunistic in where and when they foraged. That is consistent with the fact that the negative correlation with food supply was stronger for density of adult males than for density of adult females.

Hence, a reviewer must raise 2 questions: (1) To what extent were the variations in adult density responses to variations in food supply, reflecting only a shift in the total number of adults foraging on Rogers's study area, but not a shift in the total number present over the whole habitat? (2) Alternately, to what extent were the negative correlations between food supply vs. adult density due to coincidental variations in the number of bears maturing into adulthood minus attrition of older adults, due in part to hunting pressure? Hunting pressure may or may not have been affected by changes in plant phenology associated with changes in food supply for the bears. These questions can only be posed, not answered, on the basis of available data on Minnesota black bears.

Relative Impacts by Food Supply vs. Adult Male Density: Those questions aside, let us now proceed to the second issue of how much impact variations in density of adults could have had on the amount of food obtained per bear. Whereas density of adults varied over a range of only ±25% (±18% SD), food supply varied over a range of at least ±200% (Rogers, pers. comm.). So any effects of density on the average amount of food potentially available per bear would have been negligible compared to effects by variations in food supply per se.

Apparently, the only way that variation in density of adults could have had much effect on the amount of food actually obtained per bear is not scramble competition, but contest competition, by controlling not the relative amounts of food potentially available for consumption, but amounts actually available, perhaps by controlling access. For example, a single large male might control a small garbage dump or other localized food source, thereby depriving competitors of much more food than the male consumes personally (Rogers, 1977, pers. comm). This effect might be greatest when natural foods are scarce, thereby aggrevating such shortages for at least the lower ranking members of the population. Rogers did not discuss whether such contest competition had any obvious effects on the amount of food obtained by subordinants on his study area. But the wide dispersion of berry patches, the primary food source, makes that doubtful. Hence, for that particular population, the amount of food obtained seems to have depended far more on variations in food supply than on variations in density or biomass of adults. The same may have been true in the Idaho black bear populations studied by Beecham (1980a,b; see Chapter 7:III.C).

10:II.B.2. Yellowstone Grizzlies

For Yellowstone grizzlies too, there are difficulties in separating causation from mere association in correlation results, of distinguishing relative impacts on population dynamics by variations in food supply vs. biomass or density of a population or subpopulation. Results presented so far reveal that reproductive and recruitment parameters were positively correlated with the food supply index and negatively correlated with biomass and density, as one would expect. But to what extent were these demographic parameters controlled by food supply vs. biomass/density--for instance through their respective effects on food supply per unit bear mass or per bear?

Recall that correlations with food supply per unit bear mass were stronger than those with supply per bear ($P{:}1t < 0.001$), which were stronger than those with food supply per se ($P{:}1t < 0.01$).

$$r: \quad FS/BM > FS/N > FS$$

This certainly suggests that both food supply and biomass/density affected demographics. But the differences in strengths of those correlations are so small as to suggest that for Yellowstone grizzlies, as for Minnesota black bears, food supply exerted the greatest influence. This is also suggested by the fact that food supply per unit bear-mass was about twice as strongly autocorrelated with food supply as with biomass (Table 10:1). The difference in autocorrelations for supply per bear was even greater--in part because

Table 10:1. Autocorrelations between food supply per unit bear mass and per bear vs. population biomass and density for Yellowstone grizzlies.

	Food Supply (FS)	Population Biomass (BM)	Population Density (N)
Food supply per unit bear mass (FS/BM)[1]	0.993 0.0001	-0.551 0.04	
Food supply per bear (FS/N)[1]	0.997 0.0001		-0.050 0.88
Total food supply (FS)[2]		-0.430 0.19	-0.067 0.84

[1] Significance levels for 1-tailed tests.

[2] Significance levels for 2-tailed tests.

food supply might have been negatively correlated with population biomass, but not with population density.

How then might one account for the fact that most demographic parameters were correlated with biomass/density, particularly for adult males, more strongly than with food supply (Table 10:2)? Did biomass/density actually have a stronger impact; or was it merely a better index of nutrient-energy balance?

As noted in above in Section I.A, most censusing of the YNP grizzlies was done at sites of concentrated food, garbage dumps. Data from a number of black bear populations (e.g., Hatler 1967; Rogers et al. 1976) indicates that bears tend to aggregate at dumps more during periods when natural foods are scarce. If the same was true for YNP grizzlies, one might expect to find a negative correlation between supplies of natural foods vs. concurrent mean number of bears, especially adult males, feeding at dumps each year. Whether that would bias censuses for adult males or any other age-sex class would depend largely upon (a) what proportion of them was _not_ individually identifiable, and also upon (b) how consistently each individual was known to be within YNP, such that it could be counted as a resident rather than as a transient visitor from a peripheral region of the Yellowstone Ecosystem.

According to J. Craighead (pers. comm.), some bears were not seen during some years, despite being seen during preceeding and following years; this was most common for adult males--as has also been observed among Canadian grizzlies (Pearson 1975; Miller et al.

Table 10:2. Comparison of simple correlations for parameters of reproduction and recruitment vs. food supply with simple correlations vs. density of adult males and vs. multiple correlations for both sets of factors for Yellowstone grizzlies, 1959-70.*

Parameter	Density of Adult Males (#AdM)	Food Supply		#AdM & Food Supply
		w/o 1969	w/ 1969[1]	
Cub litter size (#C/L)	-0.607	0.823	0.831	±0.904
	0.02	0.001	0.0004	0.0006
Whelping level (#L)	-0.360	0.166	0.165	±0.360
	0.12	0.32	0.30	0.27
Whelping rate (%WR)	-0.537	0.235	0.232	±0.538
	0.04	0.24	0.23	0.11
Interbirth interval	-0.569	0.722	0.717	±0.742
	0.03	0.01	0.008	0.02
Cub density (#C)	-0.575	0.493	0.483	±0.617
	0.03	0.06	0.06	0.07
Cub sex ratio (%MC)	-0.614	0.218	0.215	±0.636
	0.02	0.26	0.25	0.06
Density of male cubs (#MC)	-0.639	0.341	0.334	±0.640
	0.015	0.15	0.14	0.06
Density of female cubs (#FC)	0.435	0.111	0.112	±0.638
	0.09	0.37	0.36	0.06
Cohort size at age				
0.5 yr in yr t	-0.575	0.493	0.483	±0.617
	0.03	0.06	0.06	0.07
1.5 yrs in yr t+1	-0.717	0.356	0.379	±0.718
	0.01	0.16	0.13	0.04
2.5 yrs in yr t+2	-0.850	0.479	0.479	±0.850
	0.002	0.08	0.08	0.01
5.5 yrs in yr t+5	-0.658	0.787	0.787	±0.802
	0.08	0.02	0.02	0.11

Table 10:2. (Continued).

Parameter	Density of Adult Males	Food Supply		#AdM & Food Supply
		w/o 1969	w/ 1969	
<u>% Recruitment rate between ages</u>				
0.5 - 1.5 yrs	-0.701	0.506	0.516	±0.720
yrs t to t+1	0.01	0.07	0.05	0.04
0.5 - 2.5 yrs	-0.884	0.595	0.595	±0.891
yrs t to t+2	0.001	0.03	0.03	0.004
0.5 - 5.5 yrs	-0.532	0.692	0.692	±0.704
yrs t to t+5	0.14	0.04	0.04	0.18

* Values given are r and P:1t.

[1] Recall that no data were available on garbage supply during 1969. So no figure could be calculated for total food supply then. Nor could an estimate be made for 1969 garbage supply except by interpolation from the relationships between food supply indices vs. parameters of reproduction and recruitment for other years. That was avoided in Chapter 5 in case inclusion of such an interpolated figure would exaggerate the correlations between those variables. However, now that those results have been presented free of any such exaggeration, an interpolated estimate for 1969 garbage supply has been included to faciliate comparison of relative strengths of correlations with parameters of reproduction and recruitment by food supply vs. by density of adult males. That 1969 value for garbage supply was estimated from the plot in Fig. 4:7, which relates values for litter size vs. climate during 1968-70, while dump closure was underway. The difference in mean litter sizes before vs. after closure presumably reflects primarily the decline in garbage supply. Mean cub litter size in 1969 was about 67% of the way between the 1968 and 1970 sizes, that is about 33% above the 1970 size. So garbage supply in 1969 was estimated as 33% of the difference the 1968 vs. 1970 supplies. The estimate for 1969 garbage supply was added to the natural food supply index, yielding the 1969 index for total food supply, which was then used to calculate the simple correlations with parameters of reproduction and recruitment for column 3 of this Table, where its inclusion had little effect, and of multiple correlations for column 4.

1981) and Tennessee black bears (Pelton, pers. comm.). Hence, as mentioned earlier, census figures on adult males tend to be less reliable than those for females and for unweaned males. Census figures for subadult males also tend to be less reliable, partly due to the fact that the number of transients passing through a study area during the course of a year can considerably exceed the number present at any one time (e.g., Beecham 1980a,b). But it is not clear whether the Craighead team counted bears as members of the population during those years when they were not seen and may have been absent from the study area. Nor was information published on what proportion of the adult males could be identified individually.

In any event, _if_ much of the apparent flux in density of adult males from year to year was an artifact of variation in dump usage, then one would expect to find a negative correlation between natural food supply vs. apparent density of adult males. A similar correlation might be expected _if_, during periods of natural food scarcity, there was an increase in mobility or use of open areas by bears during daylight hours, while searching for food, as has been observed in other bear populations (Drahos 1951; Hatler 1967; Rogers et al. 1976; Amstrup & Beecham 1976; see also Jonkel & Cowan 1971; Beeman & Pelton 1980). For that could have increased censusing efficiency even in the backcountry.

The only available index of natural food supply in YNP is that derived from Picton's (1978) climatic index. So the only way of testing these hypotheses in even a preliminary way is by checking for a negative correlation between density of adult males each summer vs. climate index for the preceeding winter-spring. Indeed, that index is negatively correlated with density of adult males. But the correlation is too weak to be reliable (r = -0.228, P:1t<0.25). Furthermore, the fact that density of adult males was less strongly correlated with climate index for the preceeding winter-spring than with that for the next winter-spring (r = -0.372, P:1t<0.25) suggests that both of these correlations are spurious. For, while density of adult males in the summer of year t (e.g., 1961) might have been affected by climate during the past winter-spring (e.g., 1960/61), it could not have been affected by climate during the future winter-spring (e.g., 1961/62). Density of adult females also showed only weak, probably spurious, negative correlation with the climate index for the past winter-spring (r = -0.349, P:2t=0.27) and the future one (r = -0.347, P:2t=0.30). For adult biomass, the correlations are, respectively, r = -0.250 and -0.339 (P:2t$\leq$ 0.43). Hence, these results provide no evidence that, for YNP grizzlies as possibly for Minnesota black bears, shifts in climate indirectly caused variations in density and biomass of adult males or females, whether through effects on supply of natural foods or otherwise. Even if such correlations actually existed between natural food supply and distribution of adult males, these results suggest that they were too weak to account for the strong negative correlations between parameters of reproduction and recruitment vs. density/biomass of adults.

The hypothesis that variation in density or biomass of adults was an artifact of variation in food supply also leads to a prediction of a positive correlation between garbage supply vs. density/biomass of adults, especially adult males. In fact, that is just the opposite of what was found. There were negative correlations between garbage supply vs. densities of adult males (r = -0.555, P:1t=0.96) and possibly females (r = -0.276, P:1t=0.80), as well as with adult biomass (r = -0.539, P:1t=0.96). Density of adult males in the population tended to be highest during years when garbage supply (May-September) was lowest, not highest. Garbage supply increased, more or less steadily from 1959-68, then declined sharply during 1968-71 as bears were progressively denied access to garbage at dumps (Chapter 4:II.C). Density of adult males was relatively high during the 1959-60 and 1968-70. It is doubtful that this negative correlation between adult male density vs. garbage supply represents any direct response by adult males to garbage supply.

Other possibilities to consider include the following:

1) Did adult males avoid dumps when garbage was most abundant, in order to avoid the greater disturbance by humans and vehicles bringing the garbage? Bledsoe (1975) remarked that older, more wary bears had a tendency to avoid McNeil Falls during the daylight hours, concentrating their fishing during the crepuscular and dark hours. Although fishing was least productive then, darkness maximized concealment. This was particularly noticable among adult males, perhaps because of greater aggressiveness by hunters towards them.

"Most bears seemed unaffected by our presence, although large males avoided the falls when more than three or four people were present; a limited number of other bears would not cross to the near side of the river" (Egbert & Stokes 1976:42). Greater wariness by larger, older black bears was also remarked by Frame (1974) at Olsen Creek and Glenn & Miller (1980) at Chignik-Black Lakes. So too, in 1972, rangers at Brooks River in Katmai National Monument warned me and other visitors that the most aggressive bears fished at night.

2) When garbage was more abundant, were adult males able to concentrate their foraging at dumps during periods (e.g., of the night) when observers were absent, and thus appear to be less abundant?

3) Was the apparent increase in abundance of adult males associated with dump closure due to the consequent change in foraging habits? For example, did adult males become more mobile, particularly during daylight hours, thereby facilitating censusing and increasing its efficiency?

4) Did control action removal of some adult males from the core habitat permit others to immigrate from the periphery of the Ecosystem, giving the impression that more had been present all along?

Presumably due both to garbage supply and density of adult males, density of immatures, and thus density of the whole population was strongly positively correlated with concurrent garbage supply (r = 0.651, P:1t=0.02). There is no obvious way that this could be a sampling artifact. It is not known to what extent variations in densities of immatures vs. adults account for the monthly (June-September) variations in densities of grizzlies feeding at the YNP dumps, as reported by Hornocker (1962) and which were so highly correlated with garbage supply (r = 0.988).

10:III. SUMMARY

1) Although some critics suspect evidence of density dependence among YNP grizzlies of being spurious, analysis of available data yields negligible support for that suspicion. The first hypothesis considered and dismissed argued that apparent density dependence might be an artifact of dump avoidance by family groups and subadults when adult males were most abundant in the population, and thus presumably at the dumps.

2) Then, attention was focused on other hypotheses about how variation in density of adult males might have been largely an artifact of conducting censuses at dumps. This artifact was hypothesized to arise from either or both of 2 factors:

2a) The grizzlies, especially adult males, may have tended to be more visible when natural food was scarce, due to (a) greater mobility and usage of open areas during daylight hours, and to (b) greater usage of dumps.

2b) The grizzlies, especially adult males, may have tended to use dumps in direct proportion to amount of garbage available there.

The former hypothesis was tentatively dismissed because there were only slight, non-significant, apparently spurious, negative correlations between the index for natural food supply vs. density of adult males. The latter hypothesis was dismissed because densities of adult males and females were negatively, not positively correlated with garbage supply. Hypotheses were proposed that might help to account for those negative correlations as artifacts. But available data are not adequate for testing them.

3) It is re-emphasized that unless adult males are individually identifiable, their density is particularly difficult to census reliably. The fact that fluctuations in density and biomass of adults and in biomass of the whole population were due primarily to fluctuations in density of adult males certainly warrants caution in concluding that the apparent density dependence was real. But even with that caution in mind, available data favors the hypothesis that the apparent density dependence is real, over the alternative hypothesis that it is an artifact of sampling bias.

CHAPTER 11

DISCUSSION: DENSITY DEPENDENCE RELATIVE TO SOCIAL BEHAVIOR

Recall that for Yellowstone grizzlies, reproduction and recruitment were negatively correlated with density and biomass of adults, especially males, and with adult sex ratio. For example, when density of adult males and adult sex ratio were high, few cubs were produced, mainly daughters. Those cohorts had low rates of recruitment from age 0.5 year to ages 1.5, 2.5, and 5.5 years. By contrast, density of adult males was less strongly correlated with _concurrent_ recruitment of cohorts between ages 2.5-5.5 years and uncorrelated with _concurrent_ recruitment between ages 0.5 to 1.5 and 2.5 years. Those results shall now be interpreted in terms of social behavior of the bears, based on information from this and other populations of bears or other taxa.

11:I. _HABITAT COMPETITION_

Observations of relationships between adult males vs. subadults, mainly on black bears in Minnesota (Rogers 1977) and Alberta (Young & Ruff 1982) indicate a tendency for emigration rate by subadults, particularly males, to be directly related to density of resident adult males. _If_ that same kind of social relationship existed among Yellowstone grizzlies, one would predict a tendency for attrition rates among juveniles and especially subadults to have been directly related to _concurrent_ density of adult males.

Data on interbirth intervals indicates that at least half the cub litters were weaned and dissociated from their dams by age 2.5 years. So effects of adult male density should have had considerable impact on concurrent recruitment rates between ages 2.5-5.5 years. Perhaps, that is why density of 3-&-4-yr-olds was negatively correlated with concurrent density of adult males ($r = -0.485$, P:1t=0.06), whereas densities of yearlings and 2-year-olds were not.

11:II. FOOD COMPETITION

If the apparent density dependence for Yellowstone grizzlies arises in part from intraspecific contest competition for food, then it makes sense that food supply per unit bear mass should be a better indicator than supply per bear. For, again, supply per bear mathematically weights each age-sex class of bears (cubs, yearlings, adults, etc.) equally, regardless of competitive ability. By contrast, supply per unit bear-mass estimates impacts by each age-sex class as being directly proportional to mean body mass for the class. This gives greatest emphasis to the most massive bears, those that may not only have the greatest per capita nutritional requirements, but which are most dominant in contest (confrontation) competition. If smaller bears require more food per unit body mass than do adult males, as a consequence of a higher basal metabolic rate (Kleiber 1961), that would make them suffer all the more from having food usurped by more dominant individuals.

The general relationship between body size vs. dominance status, with adult males and secondarily adult females being most dominant in food competition, has been best documented at sites where food is locally concentrated (Hornocker 1962; Stonorov & Stokes 1972; Frame 1974; Rogers et al. 1976; Rogers 1977; Egbert & Luque 1975; Egbert & Stokes 1976; Garshelis & Pelton 1981). Egbert & Stokes (1976:53) reported that at McNeil Falls, "The main consequence of social status was that it determined when and where an individual bear could fish, and in large measure, its ratio of fishing success." It also appears to play a major role in mating success, since larger males usually succeed in displacing smaller ones, although some dominant males are so aggressive that they lose opportunities to impregnate females while engaged in contests with rival suitors (Hornocker 1962). Researchers have likewise presented evidence of competition for habitat, in that dominants seem to exclude subordinants from certain areas (Jonkel & Cowan 1971; Kemp 1972, 1976; Pearson 1975; Rogers 1977, 1983; Lindzey & Meslow 1977b; Garshelis & Pelton 1981; Young & Ruff 1982).

Food supply per unit biomass represents "sharing" of the food in a uniform ratio of food mass per unit body mass, regardless of social rank. The above-mentioned observations on competition indicate that a more realistic model would represent dominants as obtaining more (preferred) food per unit body mass than subordinants do--at least from sites where the food is concentrated or where there is spatial exclusion of subordinants from resources. Furthermore, food competition is not the only source of density dependent effects. One should also consider costs to dams with cubs of avoiding prime feeding sites, combat injuries, exile of subadult sons, "murder" of offspring, and perhaps psycho-physiological distress. Conversely, the positive correlation between ability to compete for food vs. body size, could be partially compensated by the inverse relationship between metabolic rate per unit body mass vs. total body mass (BM), with cubs needing correspondingly more food per unit body mass than do adults. According to Kleiber (1961),

$$MR = 70*BM^{0.75}$$

where MR = total basal metabolic rate (Kcal/day). Hence, models of relationships of food supply per bear and per unit bear-mass might eventually be further refined by weighting density or biomass terms according to both dominance rank and metabolic rate.

If density and biomass of adults were uncorrelated with total food supply, then variations in supply per bear and per unit bear mass might fully reflect variations in both food supply and density/biomass. However, to the degree that the total food supply index was negatively correlated with density/biomass, their respective influences on correlation coefficients would not be "additive", but overlapping and thus mutually obscuring. Indeed, there were negative correlations between the total food supply index vs. adult densities (males: $r = -0.492$, $P{:}2t=0.12$, $n=11$; females: $r = -0.402$, $P{:}2t=0.22$, $n=11$) and adult biomass ($r = -0.498$, $P{:}2t=0.12$, $n=11$). Overlapping effects of food supply vs. density and biomass might explain, at least in part, why indices for food supply per bear and per unit bear mass were little better than was food supply alone as predictors for parameters of reproduction and recruitment. (Fig. 11:1)

11:III. ELIMINATING AND/OR EATING CONSPECIFICS

11:III.A. Observations

Although tales of bears killing one another are common in folklore, actual reports are so scarce that few generalizations can be drawn. Individual instances have already been listed and discussed for black bears by Rogers (1983) and for polar bears by Taylor et al. (in press). So the only detailed review given here is for grizzly bears. Interpretations concerning all 3 species shall be considered afterwards.

1) (a) Seton (19211:102) cited a report in Outdoor Life (July 1913:21-24) by L. L. Bales. On October 19, 1912, Bales found tracks in snow revealing that a large bear (estimated at about 1,000 pounds) had followed a dam and cub, eventually attacking and injuring the cub and its protective mother. Injuries to both cub and dam were confirmed after Bales killed all 3 bears. (b) Seton also reports a case of a juvenile being killed and eaten by another bear of unknown sex and age; this was during winter.

2) Couturier (1954) reviewed cases of male European brown bears wounding and killing one another during the breeding season (Mundy & Flook 1973:13).

3) Schoonmaker (1968:59) quotes a report by Wm. H. Wright (1909):

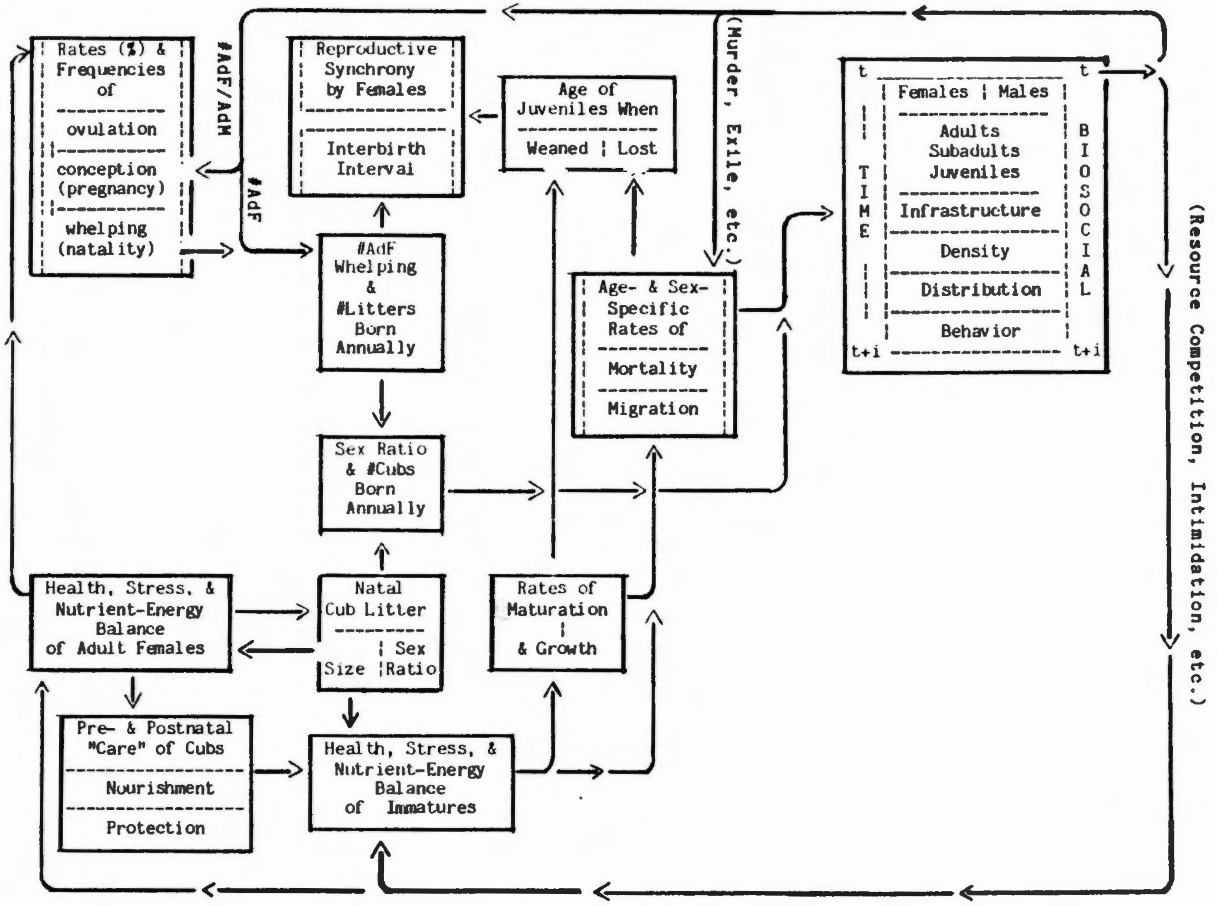

Fig. 11:1. Biosocial influences on reproduction, survival, and migration in a bear population.

immediately began eating the first and could not be driven off by being hit with rocks or by the sound of nearby rifle shots. (b) In the autumn of 1970, while flying, a large bear was seen eating a cub; the mother and another cub were hiding in brush nearby.

8) Glenn et al. (1976:387) reported 3 instances of cub loss near McNeil Falls on the Alaska Peninsula.

> In one instance a female with three cubs was carrying a salmon from the river to an alder patch on higher ground. One cub in the lead took a different trail than the others and was not seen again. The female was later seen with the other cubs and never appeared to be searching for the third cub. In another instance, three cubs became separated from their mother when she was attempting to drive off a large male. She found one cub immediately and another 3 days later. After a week, she still had only the two cubs. No other females were observed with an extra cub. In the third instance, a dead cub was found at a feeding area with a large wound in the ventral portion of the neck, apparently inflicted by another bear.

The latter victim is probably same one which was elsewhere described as a 2.5-year-old female that apparently died from a bite which had crushed the esophagus and perforated the pharynx, and whose carcass had been partly consumed (Egbert & Luque 1975; Egbert & Stokes 1976).

9) In 1972 at Katmai National Monument, on the Alaska Peninsula, National Park Service personnel told me about the death of a medium-sized bear that had been was fishing along Brooks River. A larger bear, presumably an adult male, emerged from the forest and attacked immediately, literally tearing the smaller bear to pieces. This incident was filmed and described to rangers by a fisherman.

10) Also at Katmai, George (1979) observed the disappearance of a cub whose mother had left it ashore while she fished in Brooks River. Murder by an adult male was assumed.

11) According to Pearson (1975:41), for the southwestern Yukon Territory, strife during the breeding season may result in death of some males. But the only case of death in what "should have been a low intensity confrontation" involved a bear which had recently been drugged and tagged. Although it might have still been under the influence of the drug when the encounter occurred, circumstantial evidence is said to make that doubtful.

12) Pearson (1975) also reports the case of a large adult male killing an adult female.

> On October 20 an adult boar was captured near a known denning area on a south-facing slope at 1,300 m. There was no snow on the ground. The boar had dug a mature sow out of a den on the open slope and killed her. We postulated that the adult boar was preparing a den and had discovered the sow already occupying a den site on the preferred slope. [p.51] [There may have been] competition for a denning site. [p.41]

13) For the Northern Yukon Territory, Pearson (1976:257) reports that during 1973,

> A 6.5-year-old male, weighing 147 kgs was killed by a much larger (272 kgs) 9.5-year-old male. The smaller animal wore a radio collar and was killed between September 20 and 27 along the Babbage River. The larger animal had eaten much of the carcass, cached the rest along the river bank, and remained close by in the willows. Although the larger animal was captured, no signs of physical damage were in evidence on its body. Several other cases of suspected predation occurred but prima facie proof was not obtained.

14) J. Craighead & F. Craighead (1967) reported 4 cases of infanticide among Yellowstone grizzlies. J. Craighead later (p. 245, in Herrero 1972a) reported additional incidents, noting that most juveniles were killed by large males in the spring, not all in the vicinity of dumps.

15) J. Craighead (p. 245, in Herrero 1972a) also reports on mortality related to intraspecific fighting among older bears.

> As far as we know, there has never been a mortality. We've found yearlings that have been killed, and severely chewed, mauled by another bear, but in all of the conflicts that we have observed we have no record of a grizzly ever killing another grizzly during combat, either during the breeding season or for favourable feeding positions at the dumps.

16) McCullough (1981:183) stated that "Park Service personnel reported finding three dead cubs killed in one night at the Rabbit Creek dump" in YNP.

17) Reynolds (1974:12) reports that in the eastern Brooks Range, an adult female with 2 free blastocysts in her uterus was killed by an adult male. He had apparently attacked while she was digging a den. When observers arrived within 30 minutes after her death, she was found to have

> been killed by a broken neck or by massive wounds along the top of the back near the hump; the male had not made any attempt to eat any flesh but had bitten the genitalia several times. When immobilized and examined the following day, the male showed no wounds from the encounter.

Tracks in snow suggested that the "male had been moving along a ridge crest and changed his direction of travel when he was 75 feet from the female." No comment is made as to whether den site competition might have been a motive for the attack.

18) Reynolds (1976:8) reported a case of cannibalism in the eastern Brooks Range. A large bear was seen eating a small bear at the mouth of a den in the spring of 1974; remains of an adult female and at least one yearling were also found. But it could not be determined whether they had been killed by another bear or had died

during winter and merely been dragged out of the den by the cannibalistic bear.

19) Reynolds (1980:22) reported that one large adult male killed at least 2 conspecifics, one a 2-year-old male, the other a cub; he may have also killed an adult female and her twin 2-year-olds. Another large male was

> observed confronting or stalking female No. 1038 and her three offspring near the Kokolik River. This confrontation lasted more than 30 minutes, with the male actively pursuing the female which snarled as she retreated.

20) Reynolds (in press) reports that on 24 May of one year, a large adult male was observed with the carcass of a cub in his mouth; later the carcass of that or a second (female) cub was found which had been partially consumed. The mother which had previously had 2 cubs was seen alone some distance away.

11:III.B. Discussion

11:III.B.1. Identity of Killers or Cannibals

Taylor et al. (in press) cite reports that polar bears of any age will scavange carcasses from conspecifics. In 1972, I saw black bear cubs eat from the carcass of their dam a few hours after she had been killed and skinned (unpubl. data). However, murder for predation or other motives seems more restricted to certain age-sex classes.

11:III.B.1.a. Adult and Subadult Females

I have found references to only 2 cases where the killer was known to be an adult female. (a) One is the case related by Murie

(1961; item 4, above), where Old Rosy killed 1 or 2 cubs of Nokonis. (b) Rogers (1983) cited a report by Arnold (1930) for YNP black bears of an adult female with cubs killing and eating the cub of another female. Additional possibilities are (c) the case reported by Troyer & Hensel (1962; item 5, above) of the killer being accompanied by a yearling, and (d) a case observed by Le Count (pers. comm. to Rogers, 1982) of a yearling female having been killed, while traveling with its dam, by an aggressor whose track size indicated that it had been an adult female or subadult male. Lindzey & Meslow (1977a) speculate that adult female black bears without cubs may be more likely than those with cubs to kill and eat cubs of other females.

11:III.B.1.b. Adult and Subadult Males

Where the killer is known, it is usually an adult male. However, there are also reports of attempted predation by subadult males. For example, Taylor et al. (in press) cited evidence of subadult male polar bears trying to attack adult females or their juveniles; in that species, subadult males are typically at least as large as adult females. However, in most cases, the killer's age and sex are not known, instead being inferred from its apparent body size, from its track size (as in the above-mentioned report by LeCount), or simply assumed.

The assumption that the killer is an adult male is often warranted by various considerations, including the following: The chance that a bear can attack or kill conspecifics without strong likelihood of serious injury from the victim (or its mother) would seem directly related to the difference in body size between the killer and victim (or its mother), just as dominance ranking among specifics is largely dependent upon relative body size. So adult males would seem more likely than subadult males or adult and subadult females to cost-effectively prey on conspecifics (see Rogers 1983). The fear shown towards conspecifics is also directly related to the size difference; even adult females sometimes seem terrified of especially large males. This anxiety is most throughly described by Hornocker (1962), Egbert & Luque (1975:433, 441), and Egbert & Stokes (1976:45-47). There is even some evidence of adult females preferring to mate with subdominant males rather than with the most dominant (Murie 1944, 1961; Hornocker 1962; Bledsoe, pers. comm.), and of especially aggressive males seeming to exert dominance "for its own sake" (see Hornocker 1962).

11:III.B.2. Identity of Victims

11:III.B.2.a. Adults and Large Subadults

Because of their normal ability to defend themselves and to flee, adults and large subadults seem unlikely victims of intraspecific predation or just murder under most conditions including direct combat over mates, food, or other resources (see also J. Craighead, item 15, above). Exceptions are usually cases where defensive or flight capabilities of the victim have been seriously impaired, for instance by hibernation, starvation, disease, injury, old age, immobilization drugs, or having been caught in a trap, according to observations by Johnson & Pelton (1980) and other researchers, as reviewed by Rogers (1983).

11:III.B.2.b. Small Subadults and Juveniles

The inexperience and smaller body sizes of young subadults and especially juveniles can make them potentially more vulnerable to attack than older, larger subadults and adults. But the magnitude of this difference in vulnerability remains unquantified. Yearlings and older juveniles may generally be well protected from aggression by larger bears as a consequence of both maternal defensiveness and their own capacity to escape. Young black bears often have access to trees which they can climb, sometimes but not always (Rogers 1983) finding refuge there where larger bears cannot reach them. Although young grizzlies can also climb, their greater use of open habitat reduces opportunities to find refuge that way (see Herrero 1972b, 1978). On the other hand, young black, grizzly, and polar bears can all flee. According to Taylor et al. (in press), by the time polar bears are yearlings, they are sufficiently swift and agile to escape from adults, particularly adult males; speed and agility in prolonged chases seem to decline with size and age through adulthood. However, cubs of the year, especially during spring and early summer, may not have the speed and agility or the wariness to normally escape from larger bears, even for long enough to be rescued by their dams, as Taylor et al. (in press) document for polar bears. They suggest that this might be one reason why dams with cubs of the year have a greater tendency than dams with older juveniles to avoid other bears, especially during spring and early summer. Similar observations have been made on both grizzly bears (Pearson 1975; Egbert & Luque 1975; Egbert & Stokes 1976) and black bears (Erickson 1965; Barnes & Bray 1967; Jonkel & Cowan 1971; Lindzey & Meslow 1977b).

11:III.B.3. Benefits From Killing or Exiling Conspecifics

The potential benefits from eliminating conspecifics involve (1) their value as food, (2) population regulation, and (3) reducing competition from them for (a) environmental resources, (b) genetic representation (inclusive fitness of gene alleles not carried by the aggressor), and (c) mates.

11:III.B.3.a. Cannibalism

Most reports of murder in polar bears involve evidence of cannibalism (Taylor et al., in press). That was true in at least half of the cases reviewed by Rogers (1983) for black bears, and about 75% of those reviewed here for grizzlies, although some of the latter cases of cannibalism could have been on grizzlies that died from other causes before being eaten, as noted in the data summaries in Section IV.C.1. In cases of murder where cannibalism was not reported, one does not know if (a) it was observed but not mentioned, or (b) perhaps observers arrived before the killer had opportunity to begin eating its victim, for instance before the victim's carcass became putrid enough to be palatable. Black bear cubs that I reared in 1972 readily ate fresh fish but preferred red meat rotten (unpubl. data). Food value could be an important motive for trying to kill conspecifics of any age and sex.

Even if cannibalism is a common benefit from killing conspecifics and perhaps a motive for doing so, its actual frequency is difficult to quantify. Aside from direct observation of killing, one may obtain evidence from tracks and other "sign" on the ground or snow or vegetation, or from body wounds. The high indicence of *Trichinella* infection in polar bears, despite low incidence in allospecific prey, is further evidence of common cannibalism in this species; but it does not reveal the relative incidences of cannibalism following (a) conspecific predation vs. (b) scavanging after death from other causes (Taylor et al., in press). Likewise, presence of bear bone or hair (other than from self-grooming) in the scat of a bear may be indicative of cannibalism, without revealing cause of the victim's death (Rogers 1983). Although cannibalism seems common in polar bears (Taylor et al., in press), it is apparently uncommon in black bears (Rogers 1983) and probably grizzlies. So incidence of conspecific predation is probably correspondingly lower in the latter 2 species. At present, we have no basis for thinking that conspecific predation results in enough mortalities for black or grizzly bears to substantially affect population dynamics.

Ewer (1973) and Packard & Pusey (in press) review evidence of cannibalism in felids, including the African lion (*Panthera leo*:

Schaller 1969, 1972; Packard & Pussey 1983; J. D. Bygott & J. P. Hanby, pers. comm. to Packard & Pusey), tiger (*Panthera tigris*: Schaller 1967), puma (*Puma concolor*: Young 1927; Lesowski 1963), and lynx (*Lynx lynx*: Elsey 1954). Cannibalism of juveniles by adult males has been reported in African lions by the above authors, and in coati (*Nasua nasua*) by Russell (1981).

Whereas one can obtain direct evidence of cannibalism, one can only indirectly, inferrentially evaluate possibilities that conspecifics are killed or exiled as mechanisms of (1) population regulation, or of (2) competition for (a) environmental resources, (b) genetic representation, or (c) mates. Evaluation requires that one consider the alternative theoretical explanations and predictions deduced from each hypothesis, then compare those predictions with observations. Since most of those observations were not made with the express purpose of testing these hypotheses, they are not entirely adequate for the purpose, and the hypothesis tests are correspondingly tentative.

11:III.B.3.b. Population Regulation

"Regulation" of a population can be defined in various ways. But the core concept seems to be maintenance of a stable mean with only brief deviation from that mean. This mean can refer either to density per se (N), or to density relative to habitat carrying capacity (K), i.e., habitat saturation (N/K). Although regulation usually implies negative feedback, that is not universal. Indeed, regulation is sometimes used in the looser sense of just impairing population growth rate when density is already high, without any implication that growth rate is enhanced when density is low.

Suggested mechanisms of population regulation in bears include (a) killing conspecifics, (b) evicting them from prime areas for foraging/hunting or denning, and (c) completely exiling resident rivals from the area, as well as repelling potential immigrants. All 3 mechanisms seem to regulate or at least limit density to some degree in grizzly and black bears, with their fairly stable terrestrial home ranges. But exile of subadult males seems unlikely to be an effective means of population regulation in the more nomadic polar bears, especially when they are adrift on sea ice (Taylor et al., in press). Thus, killing and evicting victims from areas of resource concentration might have relatively greater importance for population regulation in polar bears than in grizzly and black bears.

Various authors provide evidence that emigration by subadult males increases during famines (see Hatler 1967; Rogers 1976, 1977, 1983; Beeman & Pelton 1980). Since they are among the lowest-ranking bears, emigration itself does not reveal whether negative density dependent mechanisms are accentuated during famine. Unanswered questions include the following: During famines, to what extent are there changes in levels of (a) murder and cannibalism (see Rogers 1977, 1983); (b) hoarding—i.e., denying competitors access to more food than the dominant alone can consume; (c) frequency, duration, and intensity of combat and intimidation bouts; (d) other anti-social behavior; and (e) stress, anxiety, and wariness. Results presented here for YNP grizzlies are certainly consistent with the hypothesis of negative density dependence being accentuated during famine; but the negative correlations between food supply vs. density of adults, obscure any effects of food supply on per capita density dependent impacts by adults.

Note too that while such mechanisms of population regulation might _not_ be explicable in terms of individual selection, their role in direct competition for resources and mates and in cannibalism might fortuitously contribute to population regulation. The general question of population regulation via infanticide is discussed by Brooks (in press).

Results on YNP grizzlies cannot be used to assess how negative density dependent impacts might have changed as a function of food supply. For all evidence of negative density dependence is based on negative correlations between parameters of reproduction and recruitment vs. density and/or biomass of adults or of the population. Indeed, one cannot even fully separate effects of food supply (FS) from those of population biomass (BM) because of the negative correlation between FS vs. BM ($r = -0.430$, P:2t=0.19). Had there been a positive correlation between FS vs. BM, they would have tended to compensate for one another's effects, lessening their individual correlations with parameters of reproduction and recruitment. By contrast, since they are negatively correlated, they would have tended to compound one another's effects. So _part_ of the positive correlation between parameters of reproduction and recruitment vs. indices for food supply and nutrient-energy balance could really be due to negative density dependent effects, or vice versa.

Bunnell & Tait (1981:89) have theorized about selection pressures favoring the predominant role of adult males in population regulation among bears.

> There may be value in concentrating the mechanism in the most stable portion of the population. Older male bears are subject to very few forms of mortality and thus provide an ideal regulatory mechanism. If, as field observations and simulations suggest, older male bears are the regulatory mechanism, there are important implications to harvest and control. Removal of the older males represents an unnatural or at least unusual, form of mortality, and one that greatly reduces the effectiveness of intrinsic control. (p.89)

Not only might aggression by adult males tend to limit density of other adult and subadult males, but negative feedback via density of adult males could itself cause self-compensatory oscillation in population density and infrastructure (McCullough 1981).

11:III.B.3.c. Competition for Environmental Resources

If conspecifics were killed or exiled from an aggressor's home range, this could reduce competition for resources only if the victim were not soon replaced by another rival--in which case, the aggressor would not enhance even its inclusive fitness unless the new rival were more closely related than the victim. As discussed in Section IV.B., there is considerable evidence for black bears that aggression by adult males can exile subadult males or prevent them from immigrating to the aggressor's home range (Jonkel & Cowan 1971; Rogers 1976, 1977, 1983; Kemp 1976; Young & Ruff 1982; Garshelis & Pelton 1981); the same is probably true in grizzly populations, particularly those where adult males are not very nomadic. Although I have found no reports of adult male bears being exiled or being prevented from immigrating by rival males, this too may occur. In some habitats, there is great overlap among ranges of adult males (Table 11:1). However, in other habitats, there seems to be little overlap of summer/spring home ranges. We do not yet fully understand the respective roles of aggression vs. avoidance of conspecifics in limiting home range overlap (Stringham, in press). Although there is abundant evidence of adult males fighting and wounding one another, at least during the breeding season, there are few reports of losers dying as a consequence (Couturier 1954; Hornocker 1962; J. Craighead, p. 245, in Herrero 1972a; Stonorov & Stokes 1972; Egbert & Luque 1975; Egbert & Stokes 1976; Pearson 1975, 1976; Bledsoe, pers. comm., 1975).

Despite the well-documented role of adult male aggression in limiting density of other males, it may not limit density of females. Rather, density of females may be limited mainly by interactions among the females themselves. Even in habitats where females share their home ranges mainly with kin females (as well as with young sons and adult males), one cannot yet be sure that such sharing leads to higher densities of females. Shared home ranges might be comparatively larger; Rogers (1976, 1977) describes home range/territory expansion by females who have bequeathed part of their former range to daughters. Likewise, loss of an adult or subadult female might cause her surviving kin to compensatorily reduce sizes of their home ranges or to show increased tolerance towards home range overlap by less closely related females. These possibilities are all in need of further study.

Even in the case of competition for a very limited resource, such as carrion or a den site in a region where good sites are scarce, competition between an adult male vs. an adult or subadult female might be served as well by simply evicting her as by killing her, unless (a) she was not a potential or recent mate, (b) killing substantially reduces competition against his recent mates and offspring, or (c) he intends to eat her or any offspring accompanying her. I have found only 8 reports of adult females being killed by conspecifics among black bears (Rogers 1983) and grizzlies (Section II.C.2.b). In 5 of those, either the female or her offspring was reported to have been eaten; in at least 1 of the other cases, arrival of the observers might have prevented cannibalism; finally, no statement was made in either of the last 2 cases of whether or not cannibalism occurred. In any event, cannibalism occurred in at least 62% (=5/8) of these cases; even considering the small sample size, that ratio suggests that cannibalism is a major benefit and perhaps motive for attacks on adult females by adult males; whether the other possible benefits listed above have sufficiently high cost-effectiveness to warrant attacks in lieu of cannibalislm cannot yet be determined.

11:III.B.3.d. Competition for Genetic Representation

Presumably, a bear could enhance its inclusive fitness by eliminating non-kin from the vicinity of its home range, to the extent that (a) this reduces represention in the gene pool of alleles not carried by the aggressor, but (b) does not compensatorily reduce current or future benefits from exogamy (outbreeding). We do not yet know the optimal degree of genetic unrelatedness among potential mates, and thus cannot predict circumstances when competition for genetic representation might favor vs. disfavor elimination of a potential mate. But one would expect it to favor elimination of any conspecific that is not a potential mate (or offspring), whether because it is too young or too old, or of the wrong sex. The benefit:cost ratio of killing or exile is probably greatest in the case of the most vulnerable, non-kin victims, for instance offspring of rival non-kin adults. Evidence that male subadults usually disperse much farther from the natal area than female subadults suggests that adult and subadult females in a locale are likely to be much more closely interrelated than the adult and subadult males (Pearson 1975; Rogers 1977; Manlove et al. 1980; Garshelis & Pelton 1981). So any reproductive rivalry via killing one another's offspring should be more common among males than females.

11:III.B.3.e. Competition for Mates

Bears are polygynous (e.g., Murie 1961; Hornocker 1962; Mundy & Flook 1963; J. Craighead et al. 1969; Herrero & Hamer 1977). Hence, mate competition among adult females may be negligible compared to that among adult males.

One way in which male bears compete for mates is by direct aggression against one another, particularly in the vicinity of an estrus female (e.g., Murie 1961; Hornocker 1962; Stonorov & Stokes 1972; Egbert & Stokes 1976). Whether males also kill one-another's offspring as a mechanism of reducing the interval until they can sire new litters by one another's recent mates can only be speculated, as follows.

In most mammals, ovulation is inhibited or prevented by pregnancy or lactation, presumably by the female's hormonal state, perhaps involving oxytocin. Lactation is maintained, at least in part, by neural stimulation received while nursing the offspring (e.g., see Bongaarts 1980). Thus, cessation of suckling and of neural feedback from it (for instance following loss or weaning of her offspring) usually terminates lactation and thus lactational anestrus/amenorrhea. So loss of a litter prior to weaning usually terminates anestrus sooner than would have been the case if lactation had continued until weaning. Whether this can shorten the interval until the dam's next fertile estrus (her IUNFE) depends partially upon whether she would normally breed only during one specific season each year. (1) If she is a seasonal annual breeder, then premature loss of a litter is unlikely to shorten her IUNFE--although premature termination of her costs of rearing the given litter might leave her in better condition when the next is produced and enhance its size or quality (and thus survivorship). (2) By contrast, if the female normally has an interconception/interbirth interval longer than 1 year, and/or can ovulate at more than 1 period per year, perhaps at any time, preweaning loss of a litter could correspondingly shorten her IUNFE. The "savings" in time could be even greater in cases where litters are lost prenatally.

It was Hrdy (1974, 1979), who first recognized the significance of infanticide for mate competition in grey langurs (Presbytis entellus) and other primates. Hrdy argued that the capacity of females to shorten the IUNFE as a result of preweaning litter loss, can be exploited by males to shorten the interval until they can sire offspring by a female who is originally pregnant or nursing a litter. Evidence of such exploitation has been reviewed for primates (Hrdy 1979), rodents (Sherman 1981), equids (Duncan 1982; Berger 1983), and carnivores (Packer & Pusey 1983, in press). Chapman & Hausfater (1979) and Hausfater et al. (in press), have developed mathematical models to clarify the relative importance of interconception interval and other factors for the evolution of infanticide as a tactic of mate competition.

Factors identified as critical by observations and modeling are (a) amount of reduction in length of the interconception interval (or, more precisely, the interval until next fertile estrus), (b) length of tenure of the adult male with the females whose offspring he eliminates, and (c) cost of killing the young. If the male is much more likely to be able to mate with the females by shortening their IUNFE and if the litters are vulnerable, then elimination of the litters will usually be favored, all else being equal.

In langurs and African lions, reproductive success of a male depends upon both (1) siring litters and (2) protecting them from other males until (a) they have have been weaned, (b) are able to evade attacks by new adult males, and (c) are self sufficient enough to cope with being evicted from the pride by the new males. Yet mean tenure of a male with a harem is shorter than that, little more than the length of a full interconception/interbirth interval. So his chances of siring offspring soon enough for them to be born and reared successfully are directly related to how soon he can mate with the females in his harem. Because these females can enter estrus soon after loss of a litter, more-or-less independently of season, the IUNFE is readily shortened by preweaning litter loss. Since unweaned offspring are relatively vulnerable to males, and one or a coalition of males controls breeding with a harem of several females, selection pressure is strong in favor of males eliminating all unweaned offspring of the harem as soon as takeover occurs. (Hrdy 1974, 1979; Bertram 1975; Packard & Pusey 1983).

By contrast, selection pressures favoring infanticide should be greatly reduced in species where (a) the interval until next fertile estrus is not shortened appreciably, or if the infanticidal male is not usually able to sire the female's next litter. Those features depend upon (a) whether the species breeds seasonally and/or annually, (b) whether the typical interbirth/interconception interval is normally single-year vs. multi-year, and (c) whether the type of mating system is monogamous, polygynous, or promiscuous. "Polygamy" is used here in reference to cases where one more or males "owns" a harem of females, in the sense of breeding with them, preventing rival males from doing so, and associating with them on a more-or-less year-round basis. By contrast, "promiscuity" is used in reference to cases where a male breeds with any available females, but does not otherwise normally associate with them; this is exemplified, for instance, by species where males hold harems only during the breeding season.

Length of the interval between time t and onset of a female's next estrus normally depends upon whether she has an unweaned litter, and if so, how old it is--to the extent that age determines when weaning occurs. Amount that the IUNFE can be shortened by preweaning litter loss would be directly related to length of the normal IUNFE for litters that survive until weaning--in aseasonal breeders. By contrast, in seasonal annual breeders, preweaning litter loss might have no effect on the IUNFE.

Hence, authors focusing on polygamous aseasonal breeders, such as lions and langurs, emphasize the importance of litter age for determining benefits to adult males from infanticide. They predict that danger to offspring from infanticide would be directly related to length of the interval until they would normally be weaned, and thus inversely related to their age.

Even for bears and other promiscuous seasonal breeders with multi-year interbirth intervals, males would gain little from eliminating the litter of a dam due to wean the litter and breed that year anyway. But otherwise, litter age may be of little importance in these species. For while the interval between litter loss and next fertile estrus might be relatively unaffected by litter age, it would be strongly dependent upon season. If litter loss occurs early enough in the year for the female to breed that year, the male who kills or evicts this litter might be likely to sire her next litter. But if litter loss occurs so late in the summer that the dam does not breed again until the next year, the male might have little likelihood of siring her next litter. These distinctions are elaborated below.

In langurs, lions, equids, and at least some of the rodents where infanticide by males seems to be a reproductive strategy, the females typically live in harem groups with their dependent offspring. One or more males live in long-term association with the harem. For example, in northern Tanzania, lion prides contain 2-18 adult females, along with dependent offspring, and 1-7 adult males. So long as infanticidal males can out-compete rival males for "ownership" of the harem, they are more-or-less assured of being sires of the next litters produced by the harem.

By contrast, in bears, adult males seldom associate with adult females outside of the breeding season. Furthermore, females are promiscuous (e.g., Murie 1961; Hornocker 1962; J. Craighead et al. 1969) and often attract 2 or more suitors to whom they submit for copulation. An infanticidal/evicting male bear is most likely to gain consequent reproductive advantage only if he can prevent her ova from being fertilized by other males when she does come into estrus. If litter loss occurs early enough in the year for her to attain estrus that year, he might be able to keep her secluded from other males, for instance at high altitude or other locations not frequented by rival males (Murie 1961; Herrero & Hamer 1977), or to dominate rivals which do appear. But if litter loss occurs so late in the year that she does not attain estrus until the following year, or if he cannot isolate her from rival males, or dominate them, the chance of an infanticidal/evicting male being the one to sire her next litter would be much reduced--perhaps so much so as to prevent either killing or evicting unweaned litters from being cost-effective unless augmented by the benefits of cannibalism, and reduced competition for resources, genetic representation, etc.

Even for alpha males, the cost-effectiveness of infanticide is questionable. One can speculate that as a male's dominance rank rises during his maturation, he would be likely to gain increasingly from eliminating litters sired by rival males. For his risks from attacking litters would decline, and his capacity to dominate rival suitors would rise, as his combative abililties rise. Yet, (a) the female may copulate with a number of males, either serially, or intermittently--for instance she might copulate with a subordinate male while the dominant male is distracted expelling other rivals (e.g., see Hornocker 1962); and (b) several females may be in estrus simultaneously. Each of those factors would tend to lower benefit:cost ratios.

Only if the entire litter is lost, will loss of cubs shorten the interval until their dam's next fertile estrus, via prematurely terminating lactational anestrus. However, even if a male succeeds in eliminating only part of the litter, females may abandon surviving singlets or more rarely twins, in favor of conceiving new, larger litters. Although there is scant data on abandonment of small litters, theoretical calculations indicate that it would substantially enhance the female's fitness (African lions: Rudnai 1973; grizzly bears: Tait 1980).

Evidence of lactational anestrus in bears has been provided by Baker (1912), Erickson (1964), Pearson (1975), and Reynolds (in press). Nevertheless, possible exceptions, as indicated by evidence of breeding by female black bears with cubs of the year, have been reported by Alt (1981), LeCount (1983), and Powell (viva voce, 1984). Observations that females can ovulate even while lactating have also been reported in swine (English et al. 1977) and humans (e.g., Frisch 1974, 1982). In swine, interruption of suckling for a few days is usually required before ovulation will occur. But that may not be necessary in humans. Frisch argues that, among humans, inhibition of ovulation associated with lactation is largely due to poor nutritional status of the mother, above and beyond any hormonal effect. However, Bongaarts (1980, 1982) presents considerable counter evidence that control of lactational amenorrhea in humans is primarily neural and hormonal. Perhaps nutrition affects the sensitivity of females to hormonal control and/or vice versa.

In any case, factors other than nutritional status of the dam also have to be considered as possible explanations for breeding while rearing cubs: (1) As Lecount (1983) points out, cessation of suckling by offspring for a few weeks, or sometimes only a few days, suffices to permit onset of estrus (Baker 1912; Erickson 1964; Reynolds, in press). So a female which is separated from her litter for several days to a few weeks, for instance while being courted by a large male, might come into estrus and conceive, yet later resume full lactation after being reunited with her remaining cubs and stimulated by their attempts to suckle. (2) The litter seen with an adult female during the same year that she conceived might have been adopted after loss of her own litter earlier that year. Adoption has been documented in all 3 species of North American bears (Grizzlies: Hornocker 1962; Erickson & Miller 1963; Russell 1967; J. Craighead et al. 1969; F. Craighead, in Herrero 1972a:82, 1979; Bledsoe 1975; Polar Bears: Vibe, cited by Jonkel et al. 1980; Black Bears: El Harger, pers. comm.). Clark et al. (1980) found for black bears that neonatal cubs introduced into the den of a dam with her own neonates were adopted. (3) The female's neuro-hormonal mechanism for preventing ovulation during lactation could have malfunctioned. Pathology is one source of individual variation in any species.

Recapitulating: Although there may be exceptional cases of dams ovulating even while lactating, cessation of lactation seems to be the normal prerequisite. That might make the dams vulnerable to elimination of their litters by potential suitors so as to reduce the dam's interval until her next ovulation and until mating can occur.

Acceptance of the hypothesis that adult males not only theoretically could, but actually do kill cubs primarily to shorten the interval until the dam's next fertile estrus would require demonstration of the following 4 points:

1) Aside from any effects due to differences in abundance and vulnerability of cubs, attempts to eliminate cub litters are as intense and frequent as those to eliminate older unweaned litters; but aggression against weaned offspring is substantially lower, with lesser attempts to kill or exile female subadults or to kill male subadults.

2) Attempts to eliminate litters are most intense during spring and early summer, when litter loss is most likely to be followed by the dam coming into estrus during that same year.

3) Infanticidal males usually try to eliminate entire litters, or at least to reduce litter size far enough, whether by murder or exile, that the mother will cease providing adequate care to the remaining offspring and may even abandon them.

4) Elimination of a female's unborn or unweaned litter increases the male's probability of siring her next litter.

Such evidence would be most convincing in cases where one could rule out alterative motives/functions for murder or exile, such as cannibalism and resource competition. Unfortunately, data are still inadequate to test the hypothesis that rigorously. Cannibalism commonly accompanies the known cases of infanticide; and dates relative to the breeding season are seldom published.

However, as a basis for first approximation hypothesis testing, let us consider what data are available: (1) The 3 cub deaths reported by Troyer & Hensel (1962) occurred in May and June. (2) J. Craighead (p. 245, in Herrero 1972a) mentioned killing of juveniles by large males primarily during spring. (3) Reynolds (in press) reports a case on 24 May. Reynolds also reports that most cub mortality involved loss of entire litters, whereas most mortality of yearlings and 2-year-olds involved only a single member of the litter. Females which lost entire litters between early May and late June came into estrus that same year, indeed within 3 weeks in the 3 cases where it was measured precisely. Two of those females had lost their litters to adult males. (4) Just as some of these cases of known infanticide by adult male grizzlies involve cannibalism, that was also true among most of the cases reviewed by Rogers (1983) for black bears and by Taylor et al. (in press) for polar bears. (5) The earliest of those reports for black bears are from mid-July (Harvesveldt 1955, cited by Rogers 1983; M. Hornocker, pers. comm. to Rogers, 1974); in the former case, redirected aggression against the cub might have been a motive; in the latter case the cub was eaten. Arnold (1930) reports a cub being killed and eaten by an adult female in late summer.

Tietje et al. (pers. comm. to Rogers, 1982) report a yearling male being killed and eaten by a 5-year-old male in early fall.

Thus, while some aspects of these records are consistent with the hypothesis of infanticide to shorten the interval until the dam's next fertile estrus, at least as many aspects are comparably consistent with hypotheses of infanticide for (a) cannibalism or (b) competition for resources or genetic representation.

11:III.B.4. Maternal Strategies to Counter Aggression by Adult Males Towards Their Offspring

Hrdy (1974, 1979), Pearson (1975), Packard & Pusey (1983), Hausfater (in press), Stringham (1983), and Taylor et al. (in press) have discussed strategies by which dams might counter attempts by adult males to eliminate their offspring, resulting in death or lowered fitness by the offspring and wastage of maternal investment. These are listed below, after minor modifications to make them more applicable to bears:

A) Prevent males from killing or prematurely exiling offspring.
  1) Attack or intimidate dangerous males
  2) Avoid dangerous males
  3) Confuse males about which one(s) sired the current litter.

B) Minimze loss of investment in young whose demise is probable.
  1) Terminate investment in the entire litter prenatally (by aborting it, "Bruce Effect"), or postnatally (by killing, ignoring, or abandoning it).

2) Adjust reproductive output in terms of size and sex ratio of the litter and investment in it, pre- and/or postnatally.

11:III.B.4.a. Prevent Males from Killing or Prematurely Exiling Offspring

Attack or Intimidate Dangerous Males: The defensive behavior of mother bears towards adult males is well known. Hornocker (1962) provides an especially insightful description for grizzlies at Trout Creek dump in YNP. There, dams "avoided close association with males whenever possible, excitedly urging or driving the cubs away from the male" (p. 58). However, "they readily attacked any male, including the [alpha and beta] that approached them or their offspring too closely" (p.44). Sometimes a male was simultaneously attacked by 2 to 4 mothers of young cubs. Adult females without offspring "paid little heed to adult males except [the alpha and beta and] those in the Aggressive class and these were avoided at all times" (pp.61-62). Although bluffs and attacks directed towards the alpha male seldom drove him away at that time, they did seem to make him more cautious about approaching family groups for the next few days.

Except for the alpha and beta, most YNP adult males usually avoided females with cubs, "and when actually attacked, usually would not fight vigorously and would slowly retreat" (Hornocker 1962:56). Despite the fact that fights between males and dams appeared furious, they were usually short, no more than 1 minute, and may have involved little intensive biting and clawing, judging from the fact that females did not show the same marks of battle as males. Adult males, particularly the older more aggressive ones, had "massive wounds and scars on the heads and necks ...[;] ears were often mutilated and completely torn off [;] ... many of them had torn and scarred lips and jaws" (Hornocker 1962:45; see also Pearson 1975; Egbert & Stokes 1976; Lindzey & Meslow 1977b; Ruff, in press).

Observers at McNeil Falls and other areas (Stonorov & Stokes 1972; Egbert & Stokes 1976; Taylor et al., in press) have reported similar defense by mother bears of their juveniles against adult males, sometimes at the expense of sustaining severe wounds. That also occurs in African lions (Packard & Pusey 1983), coati (Russell 1981), and presumably most other carnivores, just as in many other taxa. Russell discusses the importance of coalitions of adult females for protecting offspring from potentially cannibalistic adult males in the coati. Kruuk (1972) has speculated that one function of females being larger than males in the spotted hyaena (Crocuta crocuta) is to protect their young from adult males; however, it is not clear why benefit:cost ratios would favor female-biased sexual dimorphism in hyaena but not other carnivores (see Ralls 1976).

The intensity of a dam's aggressiveness towards adult males was apparently a manifestation of some more general maternal drive. Hornocker reports a direct correlation between aggressiveness towards males vs. how carefully the dams watched over their offspring, especially in the vicinity of other bears, and in how strictly they disciplined their offspring.

Avoid Dangerous Males: In addition to the tendency of dams to keep their offspring away from adult males even at aggregation sites, as noted above, dams with cubs of the year also tend to avoid areas frequented adult males, and perhaps by all other conspecifics, as has been reported in all 3 species of North American bears (Grizzlies: Strogonov 1969; Stonorov & Stokes 1972; Egbert & Stokes 1976; Pearson 1975; Black Bears: Kinney 1940; Cahalane 1947; Erickson 1965; Jonkel & Cowan 1971; Polar Bears: Taylor et al., in press). Considering the nutritive costs to females and offspring of avoiding prime feeding areas and/or times, the alternative costs of not doing so must be rather high, presumably in terms of (a) offspring mortality, as well as (b) costs of wariness and anxiety to the mother and cubs. Pearson (1975) noted that when females with cubs of the year did feed in areas (valley bottom berry patches) frequented by conspecifics, they tended to move around much more than the other bears, presumably because of nervousness. This might have reduced feeding efficiency and increased nutrient-energy expenditures for the dams. The balance of benefit:cost ratios favoring avoidance of food concentrations seems to decline as the offspring grow and mature until they are capable of escaping older bears through wariness, speed, agility, and ability to attain shelter, for instance in a tree. Avoidance of conspecifics declines between spring and fall, as cubs mature, and is even much more attenuated by the time juveniles are in their second summer.

Confuse Males About Paternity: Kin selection theory leads one to expect adult males to be least likely to kill or prematurely exile their own offspring or other close kin. Decreased aggression towards offspring of kin or past mates has been reported by Russell (1981) for coati and in various primates (Hrdy 1979). Likewise, among African lions observed by Packard & Pusey (in press), small cubs survived in only 1 case of a pride take-over by a new coalition of adult males; that new coalition consisted of males born in that same pride, all uncles of 1 of the 2 litters which survived; they were less closely related to the second litter. Indeed, familiarity with a female, especially experience having copulated with her, may be the primary means by which males in polygynous mammals distinguish their mothers, sisters, or previous mates. Hence, as Hrdy has suggested, females might inhibit aggression towards their litters by copulating with several adult males and preventing them from discerning which one(s) actually sired the litter. That might be one function of promiscuity in female bears.

11:III.B.4.b. Minimize Loss of Investment in Offspring Whose Demise is Probable

Terminate Investment Prenatally: In a variety of rodents, pregnant females abort in response to the odor of an unfamiliar male (Bruce 1959). Bruce & Parrott (1960) attributed this to the potential advantages of exogamy gained by mating with the new male. By contrast, various other authors assert that females gain from thereby terminating investment in offspring unlikely to receive investment from the new male (see Dawkins 1976) or likely to be killed by him postnatally (e.g., Labov 1981). Still others assert that abortion itself is forced by the adult males as a means of killing one another's litters prenatally, and perhaps as a means of shortening the interval until the dam's next fertile estrus (Wilson 1975; Barash 1977). Much of this literature is reviewed and critiqued by Schwagmeyer (1979). In feral Camargue horses, stallions which take over a harem of mares sometimes kill unweaned foals (Duncan 1982). Berger (1983) found no evidence of that in wild horses in America, but did find induced abortion. Whether abortion benefits the new stallions more than the mares is unclear. An important point made by Berger is that the tendency to abort was inversely related to the lateness of gestation when the mare was usurped by the new stallion (and usually forced to copulate with him). However, contrary to an hypothesis by Bertram (1975), Packard & Pusey (1983) reported no evidence of induced abortion following coups by new coalitions of males in African lions.

For bears, abortion by females in response to encountering an unfamiliar male would not seem adaptive in populations where such encounters may be fairly common and not necessarily important for survival of their litters pre- or postnatally.

<u>Adjust Reproductive Output</u>: Recall that for Yellowstone grizzlies, both density and sex ratio of cubs were inversely related to density of adults, especially males, and to adult sex ratio

(McCullough 1981; Chapter 8:II.A). When adult males were scarce, many cubs were produced, mostly sons. But when adult males were abundant, few cubs were produced, mostly daughters. Perhaps females produce fewest cubs when probability for cub survivorship is poor, and then mostly daughters, the sex least likely to be evicted by adult males and perhaps also least likely to be killed by them. Judging from correlations, changes in cub sex ratio and density seem to have been controlled more by changes in density of litters with mainly sons than by changes in litter size--suggesting that dams adjust sex ratios of their litters more by either not producing or eliminating predominantly male litters, pre- or post-natally, than by eliminating sons from litters. Evidence for adjustment of offspring sex ratio in adaptation to biosocial or environmental circumstances of the dam has already been provided for a variety of other mammals, including yellow baboons (Papio cyancephalus; Altmann 1980), Bonnet macaques (Macaca radiata; Silk et al. 1981), white-tailed deer (Odocoileus virginianus; McCullough 1979; Verme 1983) and red deer (Cervus elphus; Clutton-Brock et al. 1982).

Like number and sex ratio of offspring, mean maternal investment per offspring might be adjusted to environmental or biosocial circumstances. Among Yellowstone grizzlies, mean per capita investment may have been lowest in cohorts produced when adult males were most abundant. That is suggested by the negative correlation between circumnatal density of adult males vs. recruitment rates of the cohort between infancy and adulthood.

11:III.B.5. Related Hypotheses

Other factors that would tend to reinforce selection for negative correlations between adult sex ratio or adult male density vs. offspring sex ratio, density, or investment, are suggested by the Trivers-Willard and Fisher hypotheses.

11:III.B.5.a. Trivers-Willard Hypothesis

In polygynous species, dependence of reproductive success upon above-average capacity to compete with same-sex rivals is much stronger in males than in females (Trivers & Willard 1973; see Chapter 6:VI). For whereas even low-ranking females usually succeed in reproducing, low ranking males may sire few or no litters. In many polygynous species, competitive ability seems strongly dependent on relative body strength and other aspects of what Geist has termed "phenotypic quality." That in turn may be strongly influenced by the amount of parental investment received during the juvenile years. Hence, low-investment daughters may have almost as high a reproductive success as high-investment daughters, whereas low-investment sons may have far less success than high-investment sons. So dams should produce sons only if they can invest highly in each of them, but otherwise produce daughters. Bears seem typically polygynous in these respects. Thus, _if_ mean investment per offspring among Yellowstone grizzlies really is reciprocally related to adult male abundance and adult sex ratio, then this principle too would favor a compensatory sex ratios between adults vs. cubs.

11:III.B.5.b. Fisher's Hypothesis

Fisher (1930) argued that when adult males are scarce, relative to adult females (i.e., a low adult sex ratio), each remaining adult male produces more offspring, on average, than does each adult female. Hence, sons would be potentially more valuable than daughters to their parents' fitness. The reverse would be true if there was a high adult sex ratio. So parents should produce mostly sons when adult sex ratio is low, but mostly daughters when adult sex ratio is high.

Reciprocal sex ratios between offspring vs. adults in ungulates are discussed by Verme & Ozoga (1981) and Verme (1983), in terms of data, physiological mechanisms, and adaptive significance.

Recapitulating: For Yellowstone grizzlies during 1959-70, there were reciprocal relationships between cub density, sex ratio, and recruitment to adulthood vs. circumnatal density of adults, especially males, and adult sex ratio. These seem better explained as reproductive adjustments by dams, manifesting a strategy to avoid wasting reproductive investment due to aggression by adult males, than as direct products of adult males killing or exiling the offspring. Compensatory sex ratios and investment might also be promoted by relative values of high- vs. low-investment sons and daughters (Trivers & Willard 1973) and by the greater fitness enhancement for parents who produce offspring of the sex which is currently rarest in the population or among adults (Fisher 1930). But neither of these latter hypotheses would account for compensatory densities of adults vs. cubs. So even if the Trivers-Willard and Fisher hypotheses also apply to bears, the reproductive strategy of bears was probably shaped less by the selection pressures considered by those authors than by pressures of coping with adult male aggression.

11:III.B.6. Paternal Strategies to Counter Aggression by Rival Males Towards their Offspring

A mother bear protects her offspring directly, by aggression against other bears encountered while the juveniles are with her. She may also protect them "indirectly", by discouraging other bears from frequently her home range, even while the offspring are not accompanying her. This could be one function of her scent markings.

Adult male bears do not protect their own offspring directly, in the way the mothers do. But they may protect them indirectly when they repel adult and subadult males from immigrating, and perhaps even when they evict subadult males born on the area (Rogers 1977; Stringham 1980). Indeed, protection of cubs from invading males seems to be a primary role of resident adult males in African lion prides, one so taxing on them as to reduce their mean life span substantially (Bertram 1975; Pusey & Packard 1983). Without the protection of resident adult males, a pride is likely to soon be usurped by another male coalition. Following the coup, the cubs are almost certain to die, whether due to (a) direct attack by the new males on the cubs, (b) neglect of the cubs by their stressed mothers, or (c) possibly other characteristic factors such as redirected aggression even by kin of the cubs. Likewise, McLean (1983) reports that after resident adult male ground squirrels (*Spermophilus parryii*) were removed from 2 meadows, immigrant males killed or otherwise contributed to the demise of many offspring, raising their mortality rate much above the level typical when resident males are present to prevent immigration by rivals. If and where adult male black and grizzly bears do protect their offspring by preventing immigration of rival males, this should be taken into consideration in management strategies.

11:IV. MANAGEMENT IMPLICATIONS

If the attempt is made to manage population dynamics by controlling the density of adult males, a distinction should be made according to the type of social organization exhibited by each population and between resident vs. non-resident males.

In YNP, attrition rates of juveniles and subadults seem to have been inversely related to circumnatal density of adult males; subadult attrition rates also seemed inversely related to concurrent density of adult males. But what do those correlations actually mean in terms of interactions among the bears themselves? Sociobiological considerations suggest that aggression by adult males towards juveniles and subadults should be sufficiently discriminatory that males do little harm to their own offspring. So a more general hypothesis derived from the above result is that attrition rates of juveniles and perhaps subadults may be inversely related to density of *those adult males unlikely to be their fathers.*

The importance of this distinction lies in the question of how well adult males can distinguish which offspring they sired. If promiscuity by adult females does confuse adult males as to paternity, and if each male who copulates with a female is inhibited from eliminating her next litter, at least to the exent of not killing it or exiling the sons prematurely, then *density of adult males not likely to be the father* could differ substantially from *total density of adult males.* How much it would differ and how strongly that would affect attrition rates of immatures, would probably vary as a function of social organization.

In YNP, McNeil, and some other populations, home ranges of adult females are overlapped by ranges of many more adult males than they copulate with during estrus. Thus, their next litters are likely to be exposed to many males not inhibited by possible paternity from trying to eliminate the juveniles. By contrast, in habitats where the bears are fairly well dispersed, with stable home ranges, adult females may seldom encounter more adult males than they can mate with during a given year. So their next litters may be exposed to few adult males likely to try to kill the litters or to exile them prematurely. A more general version of the hypothesis is that danger to litters from adult males is probably directly related to the density of adult males whose home ranges overlap that of the dam, and inversely related to the dam's promiscuity.

Granted, attrition due to exile can have different effects than murder on population dynamics. But magnitude of that difference would depend upon how much rates of survival and/or reproductive success are reduced for immatures that are exiled prematurely.

Thus, one can hypothesize that the extent to which harvesting adult males would likely reduce attrition rates for immatures should be higher in populations where each female's home range is overlapped by many adult male ranges, than in those where it is overlapped by few male ranges. Indeed, in populations with little home range overlap among adult males and females, harvesting adult males resident in an area could have the opposite effect and increase attrition rates of their offspring by exposing them to immigrant males or resident subadult males likely to try eliminating the offspring, whether "for" cannibalism, reducing current and future resource competition from them, or for immediate gains in reproductive advantage (see also Rogers 1977). In regard to that hypothesis, it is noteworthy that available evidence does suggest that cub attrition rates are higher in grizzly populations where abundance of adult males has been reduced by hunters (Chapter 7:II.A). Although more study will be needed before one can quantify the relative benefit:cost ratios of different harvest scenarios and population infrastructures, and thereby test this hypothesis, it should be kept in mind even now when planning research, deriving population models, and designing management strategies.

Another management consideration involving behavior and abundance of adult males, is that governing density of adult males in core areas might be used to help govern emigration rate for subadults from those areas. Emigration from reserves might be fostered in order to provide bears to repopulate peripheral habitat, or for immediate harvest there by hunters. Conversely, emigration could reduce harvestable yield within a core area.

Although occurrence of emigration by subadults is <u>not</u> a reliable indicator of overpopulation in their natal area, it may prevent overpopulation fortuitously. Continual elimination of adult males might permit density of subadults to rise high enough so that not only direct aggression against juveniles, but also increased competition for resources, reduces rates of production and survival of juveniles within that area.

Results presented here, and especially the simulation model being developed, should provide a more precise basis than existed previously for estimating the particular density of adult males and adult sex ratio that would best promote any desired rates or levels of reproduction and recruitment. For instance, the attempt might be made to maximize levels of reproduction and recruitment until the density and infrastructure for the population are high enough that probability is at least 95% (e.g. Shaffer 1978, 1983) that the population will be able to regulate itself indefinitely without further intervention by humans, despite forseeable variations in environmental conditions.

If and when the decision is made to manipulate a population by reducing density of adult males, within YNP or any other wildlife preserve, sport hunting would not necessarily be the best way of achieving that. Even aside from the social and political consequences of permitting sport hunting of a protected population, whether inside or outside of the reserve boundaries, one must consider the effects of hunting on behavior of surviving bears towards human visitors and residents in the vicinity of the reserve. Actions which make the bears more wary of humans might indeed reduce the chance of humans accidently encountering a grizzly at close range. But it might also increase the likelihood of attack and of death or serious injury to the humans when such encounters do occur. As has been argued elsewhere (e.g., Stringham 1982), bears should not be trained to fear of humans as such, or that humans will attack without provocation, but that humans will retaliate if attacked--that the costs of attacking people or damaging property are much greater than the benefits. Means chosen for protecting people, property, and bears should not escalate tensions between people and bears but reduce them, détente. Safety for both bears and humans would seem to be better promoted by mutal respect than by mutal antagonism.

11:V. SUMMARY

1) Dominance status tends to be directly related to body size and aggressiveness. So adult males tend to be most dominant in competition for food and probably space. Adult females tend to be next highest ranking, although some adult females dominate some adult males in such competition. Dams can also deter approach to themselves and their cubs by all but the very highest ranking males. Defense against adult males is usually by single dams, but occasionally by 2 or more simultaneously.

2) Aggression by adult males tends to promote emigration by adults born locally and to deter immigration by those born elsewhere. Hence, net recruitment rate for subadults tends to be negatively correlated with density of adult males. We do not know whether aggression by adult females plays a similar role in regulating dispersal and density of subadult males or females.

3) Adult males can also affect recruitment rates of locally born offspring by (a) exiling them before they are weaned or (b) by killing them. Eliminating offspring of rival males might also benefit the aggressor through reducing competition with those rivals for genetic representation and mates--if eliminating of the unweaned juveniles increases the opportunities for the aggressor to breed with the dam. The aggressor might also benefit directly through (a) value of the victims as food, if he eats them, as well as (b) reducing current or future competition from victims for environmental resources, genetic representation, or mates.

4) Cannibalism appears widespread and common among polar bears, but uncommon among grizzly and black bears. However, even in the latter species, fights among rival males during courtship of estrus females, and other attacks on conspecifics, are sometimes fatal and occasionally followed by cannibalism. Indeed, cannibalism may be a motive for some attacks (as well as for scavanging). Killing or exiling conspecifics, usually juveniles or subadults, might also reduce competition with the aggressor for environmental resources, genetic representation, or mates, currently or in the future.

5) It is much less certain whether another motive/function for murder or exile of litters by adult males is shortening the delay until the male can breed with the dam. Eliminating a litter can terminate the dam's lactational anestrus soon enough to allow her to breed that year, only if it occurs no later than 1-4 weeks before the end of the breeding season in early summer. Yet, we have little evidence that attacks by adult males are concentrated in spring and early summer. If the female does not come into estrus again until the following year, she might have weaned her cubs by then anyway, and chances seem small that the infanticidal male will be the one who succeeds in siring her next litter. So benefit:cost ratio for infanticidal males might be poor--especially considering dangers to a male who attacks juveniles when their dam is near enough to defend them. Furthermore, the dam is sometimes killed, in which case she and/or her cubs may be eaten. Hence, elimination of a litter to shorten the interval until the dam's next fertile estrus might be a minor motive/function compared to (a) cannibalism or to (b) reducing current or future competition for resources or genetic representation.

6) Dams with juveniles tend to avoid conspecifics, particularly adult males. That is especially common when their cubs are too young to have the wariness, speed, and agility, needed to escape conspecifics, including adult males.

7) Dams may also minimize wastage of investment in offspring likely to be killed or prematurely exiled by adult males. They might do this via year-to-year shifts in (a) abundance and sex ratios of

cub litters and cubs produced, as well as in (b) investment per cub. When adult males are abundant among Yellowstone grizzlies, few cub litters and cubs are produced, mostly daughters--potential mates of the adult males, and perhaps in less danger from them than are the sons of rival males. The low recruitment rates of these cohorts over the next several years suggests that they are of below-average quality, perhaps because of receiving below-average investment per capita from the dam. By contrast, when adult males are scarce, many cub litters and cubs are produced, mostly sons, whose above-average recruitment rates to adulthood may be indicative of above-average per capita investment from the dam. This needs further study.

These fluctuations might also be governed by advantages of producing cubs of whichever sex is currently rarest in the population, at least among adults, in accordance with the theory by Fisher (1930).

Furthermore, when mothers can afford to produce only low-quality offspring, they might gain most from producing primarily daughters, whereas they might gain most from producing primarily sons only when they can afford to produce high-qualilty young, in accordance with the Trivers-Willard (1973) hypothesis.

8) Aggression by adult males thus seems to affect population dynamics in the following ways:

8a) Direct scramble and contest competition for food and other environmental resources.

8b) Killing juveniles or evicting them from proximity of their dam before they are mature enough to have a good chance of surviving independently for even the few weeks that courtship lasts.

8c) Exiling resident juveniles or subadults, mainly males, from the vicinity of the dam's range.

8d) Discouraging immigration, mainly by subadult males.

8e) Costs to dams of (1) combative and intimidative defense, (2) avoiding prime feeding areas and/or times, (3) adjusting size and sex ratio of cub litters produced, or even by pre- or postnatally eliminating predominantly male litters when adult males are abundant, to minimize wastage of investment in doomed offspring.

8f) Metabolic and behavioral costs of anxiety and wariness, such as elevated metabolic rate, physiological distress (GAS, adrenal-cortical activation, etc.), reduced feeding efficiency, and so on.

8g) Given that aggression by adult males is probably a phylogenetically old trait, one would expect defenses against it by adult females and young to minimize consequent losses of offspring and of maternal investment. Results here suggest that inverse relationships between parameters of reproduction and recruitment vs. circumnatal density of adult males and adult biomass are due at least as much to adjustments of reproductive output by dams as to murder, exile, or direct resource competition by adult males. So too, negative correlations between densities of subadults vs. concurrent density of adult males are likely to result more from forcing egress by subadults than from killing them.

9) Adult males may be inhibited from eliminating offspring of their recent mates or of any familiar female, but not of non-mate or unfamiliar females. If so, then promiscuity by an adult female might prevent her former consorts from distingishing which sired her current litter and thereby inhibit these males from killing that litter or from prematurely exiling the sons.

10) Furthermore, under those circumstances, aggression by resident adult males (a) towards intruder males and (b) perhaps even towards native subadult males, might prevent those other males from eliminating resident juveniles. This has important management implications.

11) Those implications are manifest in the following hypothesis: In habitats where adult females encounter few adult males with whom they have not copulated, or to whom they are not familiar enough to inhibit infanticide, harvesting of resident males by hunters could substantially increase immigration by unfamiliar, potentially infanticidal males. Aggression by immigrant males could in turn increase the rates of attrition of resident juveniles, as well as perhaps impairing reproduction by resident adult females. Reduced egress by resident subadult males might have similar effects. By contrast, in habitats where adult males are more nomadic, and many share the same home range with one another and with adult females, harvesting some of those males might elevate recruitment for juveniles

and perhaps rate of reproduction by the females. This hypothesis needs to be tested.

12) Ideally, game reserves should be established where harvest rate for resident adult males is low. These reserves could serve as reservoirs from which emigration by subadults and low-ranking adults would provide a steady supply of bears for harvest on the periphery, or for repopulating nearby habitat. Resident males in the reserves could be harvested at a rate optimum for population dynamics.

13) If reducing density of adult males were proposed as a means of elevating rates of reproduction and recruitment in a bear population, the advisability and best means doing so would differ according to other intended uses of local resources. In parks and other areas where danger to people from bears is a major consideration, trapping might be a better method than sport hunting for removing adult males. Although hunting might make the bears more wary of humans, and more likely to avoid people, it could also increase probability of attack resulting in serious injury or death of the humans when encounters do occur. Training of wild bears should be aimed less at producing fear of humans than respect--i.e., not fear of unprovoked attack by humans, but fear of retaliation if they are aggressive towards humans--a mood of armed equality and détente.

PART IV: GENERAL DISCUSSION

CHAPTER 12

APPLICABILITY OF THESE RESULTS TO OTHER BEARS OR OTHER TAXA

Comparison among grizzly populations revealed that parameters of reproduction are positively correlated with various indices for individual nutrient-energy balance (e.g., based on latitude, habitat type, or body weight) and negatively correlated with proportions of adults, especially male adults, in the populations. Those results substantiate and begin to quantify relationships long known or suspected for grizzly, black, or polar bears. That background information, along with the fact that these relationships already represent several bear populations, suggests that they will also be applicable to other populations of bears and perhaps other taxa. What is most likely to differ among other groups of populations of these or other taxa are not existence of the positive and negative correlations, respectively, but strengths of the correlations and specific values of the regression equation parameters. For example, the amount of change in cub litter size, interbirth interval, or any other demographic parameter per unit change in adult female body weight or in latitude (i.e. slope of each equation) might be higher or lower.

Regressions for comparison among populations fit stright lines to the data; for there was no compelling evidence of non-linearity. However, non-linearity was obvious in data on Yellowstone grizzlies and is theoretically necessary, at least at extreme values. The forms of the YNP curves were consistent enough with theoretical expectations and their fits to the data tight enough to leave little doubt but that they are realistic, not artifactual. Why then were similar curves not found from comparison among populations? That is but one of many questions which arize about how well findings on Yellowstone grizzlies censused during 1959-70 or even -81 apply to other bears, be they (1) members of the Yellowstone population (a) at that time or (b) at other times, or (2) members of other populations or species.

12:I. OTHER YELLOWSTONE GRIZZLIES

12:I.A. Uncensused Members of the Yellowstone Population in 1959-70

To what extent were the bears censused by the Craighead team, during 1959-70 primarily within YNP, representative of the entire population of the Yellowstone Ecosystem at that time? According to Craighead et al. (1974), censuses of Yellowstone grizzlies were conducted every few days during June through August each year, with an average of about 41 3.5-hour censuses per year. They were made at 5 sites through the Park, garbage dumps where the bears aggregated to feed. Bears seen only in the back-country were added to the count made at or near dumps. Since most grizzlies seen in back-country were also seen at dumps, Craighead et al. (1974) concluded that most members of the population visited dumps at least occasionally (see also F. Craighead 1976, 1979; J. Craighead 1980).

Nevertheless, as pointed out by Cowan et al. (1974) and McCullough (1981), the fact that bears seen at dumps were also seen in the backcountry does not reveal what proportion of the population in the entire Yellowstone Ecosystem was so difficult to see in the backcountry and visited dumps so rarely, if ever, that they were missed by censuses.

Hence, 2 questions were asked: (1) What proportion of the Yellowstone grizzlies were encompassed by the Craighead censuses? (2) How representative are censused bears for the entire population?

Three corresponding hypotheses have been proposed: (a) Null hypothesis: All classes of bears (e.g., classified according to age, sex, or location of each bear's activity center relative to the dumps) within the Yellowstone Ecosystem made fairly equal use of the dumps and thus had equal probability of being censused and marked. (b) There was a distinct subpopulation of grizzlies within the Yellowstone Ecosystem that made little or no use of dumps and were thus mostly missed by censuses. Dynamics of their subpopulation are not necessarily represented by dynamics of the dump-feeding subpopulation (Barnes & Bray 1967; Cole 1973); (c) There was a more-or-less continuous gradient in dump usage by the Yellowstone grizzlies, some feeding there frequently, others occasionally, and still others not at all (J. Craighead & F. Craighead 1971; J. Craighead et al. 1974; F. Craighead 1979).

12:I.A.1. Censusing Efficiency

McCullough (p. 175) attempted to answer the question of censusing efficiency through Lincoln index type calculations:

> If it is assumed that all the bears in the ecosystem are completely mixed, ..., the ratio of marked to unmarked bears dying outside the park should be the same as in the park. Therefore, the null hypothesis that there was no difference between the marked to unmarked ratios inside and outside the park can be tested. Rejection of the null hypothesis would indicate a significant number of bears did not visit garbage dumps regularly.
> A X^2 test for two independent samples, using the data described above, gave highly significant differences (for 1959 to 1967, p = 0.0013, for 1959 to 1970, p = 0.0005). The null hypothesis was rejected, and it was concluded that a significant proportion of bears in the ecosystem were not regular visitors to the garbage dumps, and hence, were not included in the censusus made by the Craighead team.

It was also on the basis of the ratio of marked vs. unmarked bears known to have died within YNP (nearly all from artificial causes) to the same ratio outside YNP, that McCullough calculated that bears censused by the Craighead team represented only 57% of those in the Ecosystem, and that total population size averaged 314. By contrast, Craighead et al. (1974) had used used the ratio of marked vs. unmarked bears killed in the Yellowstone Ecosystem and the number of live marked bears within YNP to estimate that their censuses had encompassed 77% of all grizzlies in the Ecosystem, and that total population size averaged 229 grizzlies. In either case, censusing efficiency for bears whose activities centered within YNP was certainly much higher than for the entire Ecosystem, possibly above 90%. Extremely high censusing efficiency within YNP is also indicated by the unusual consistency from year to year in the figures for the size of each cohort at ages 0.5 to 2.5 (and, by inference, to age 5.5 years), and clarity of the relationships between cohort sizes vs. food supply indices and biosocial factors.

12:I.A.2. Censused vs. Uncensused Grizzlies

Questions of censusing efficiency aside, one might also consider how bears censused might have differed from those not censused. Social and nutritive conditions at dumps differed enough from those away from dumps that this may have produced corresponding differences in reproduction and recruitment. For example, dump-feeding bears may have been better nourished and thus produced more offspring or more robust offspring. But exposure to dangerous conspecifics near dumps could have decreased offspring survival rate below that of non-dump-feeding bears.

12:I.A.3. Discrete Subpopulations vs. A Gradient

McCullough rejected the null hypothesis that censused bears were a random sample from the Yellowstone population, and interpreted that as adequate justification for accepting the alternative hypothesis that dump-feeding grizzlies constituted a discrete subpopulation. That hypothesis is supposedly bolstered by observations, mainly on black bears, that sites of concentrated foods are used primarily by individuals with adjacent home ranges and little by those with more distant ranges--as reflected by the small amount of overlap between individual home ranges especially for females--the sex with greatest home range tenure (Table 12:1). But however typical that pattern is for black bears, in is not valid for grizzlies in Yellowstone or most other populations; indeed, the only grizzly population where there is minimal overlap even for ranges of females, is the Kluane population in the southwestern Yukon Territory (Table 12:1). To the extent that a reviewer can tell from published data, gradients in usage of food concentrations are typical in grizzly populations.

During 1959-61, the number of grizzlies at the Trout Creek dump varied from about 30 in early June to 75 during mid-July and early August (Hornocker 1962), the peak of the tourist season and thus the peak in garbage abundance (Fig. 4:6). In fact, as noted in Chapter 4:III.C., variance in the garbage supply index during 1959-61 accounted for 98% of concurrent variance in numbers of bears counted by Hornocker at that dump during June-September (on the 15th day of each month). During 1964-66, when mean garbage supply was high, up to about 130 different grizzlies used the Trout Creek dump during July and August (J. Craighead & F. Craighead 1971; J. Craighead 1980).

On average, censused YNP grizzlies may have visited dumps more often and been better nourished but more stressed socially than those not visiting dumps at all. That may have in turn produced a corresponding gradient in rates of reproduction and offspring recruitment (see Chapters 4 and 6). But until Craighead et al. publish data or statistical tests for reproductive success vs. frequency of dump visitation by known grizzly bears in the Yellowstone Ecosystem, one will not be able to determine how much of a gradient there was in dump usage by the bears or its importance for population dynamics. The Craighead team's data on YNP grizzlies may well be more <u>representative</u> of bears visiting dumps regularly than of bears seldom or never visiting them. Such a gradient might bias estimates of dynamics for the entire Ecosystem population, but _not_ for the censused animals, which apparently constituted the vast majority of residents within boundaries of YNP.[1]

12:I.A.4. Non-uniform Distribution of Grizzlies Within the Ecosystem

Two more hypothese should now be mentioned: (1) Because some attrition of subadults was undoubtedly due to their egress to peripheral portions of the Yellowstone Ecosystem, at least a few survivors may have eventually returned to YNP and fed at dumps as adults. If so, recruitment rate for some adult age-classes within YNP might have exceeded 100% occasionally. (2) There might have been a gradient in infrastructure between the core of the Yellowstone Ecosystem and its periphery, with subadult males being relatively more abundant on the periphery. Although data are not available with which to test these hypotheses, non-fatal egress is important enough to have required maintaining the distinction between attrition vs. mortality in these analyses of population dynamics.

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[1] Any such bias is more likely to have overestimated population growth rate than to have underestimated it. So the rates of _decline_ in density of YNP grizzlies, following dump closure, that was predicted by J. Craighead et al. (1974) would have tended to be conservative, all else being equal.

12:I.B. Other Periods for the Yellowstone Population

Results in Chapter 5 cover periods both before and after dump closure in terms of how parameters of reproduction and recruitment responded to changes in food supply and climate. Response to climate seems unaffected by dump closure (Fig. 4:6). Indeed, loss of garbage as a major food source seems to have had effects on litter size comparable to lowering natural food supply or to increasing food requirements as a consequence of more severe climate. Regression curves derived over the full period 1959-81 may well retain applicability in the future for Yellowstone grizzlies.

By contrast, results on density dependence are derived from data covering primarily the period prior to dump closure, when the bears regularly aggregated to feed. Now that dumps have been closed and the bears are more dispersed, fluctuations in density/biomass of adults, particularly of adult males, will probably exert less impairment per capita on population dynamics. Although adults, particularly males, may still play a major role in exiling juveniles, particularly males, the rate of murder and degree of psycho-physiological stress on immatures and on adult females might well have diminished. So, while basic shapes of the curves for density relationships may not be much affected by dump closure, (a) the density dependent component of each curve (see Chapter 13:II.A) might be shifted to the right (i.e., same effect attained only at higher density), and (b) their "height" (Y-intercepts) will probably be greater (less inhibition at a given density/biomass). (c) A shift to the right in the density independent component of each curve might also have been promoted if dispersion of adult females after dump closure led to an increase in the minimum density of adult males needed to assure maximum rates of fertilization and whelping. But any such increase was probably small, judging from the finding that distribution of grizzlies within the Yellowstone Ecosystem was little affected by dump closure (J. Craighead 1980).

12:II. APPLICABILITY TO OTHER POPULATIONS AND SPECIES

12:II.A. Naturalness of Feeding Aggregations

Question has been raised as to how representative data are from a population feeding heavily from artificial food sources where the bears aggregate in high numbers--numbers so high that they are supposed by some biologists to be "unnatural." To test that hypothesis fully would require comparison of demogrphic information from Yellowstone with information from several other populations, including some where aggregations (a) at dumps involve fewer bears, (b) occur only at natural food sources or (c) do not occur at all. However, such comparative data is not yet available. Nevertheless, thorough review of available literature does clearly demonstrate that feeding aggregations are both natural and common for both polar and grizzly bears and to a lesser extent for black bears. Whereas food concentrations may draw mainly those black bears with adjacent home ranges (Jonkel & Cowan 1971), they typically draw grizzlies or polar bears from much larger areas, as indicated by the higher degree of home range overlap in these latter species (Table 12:1). Because this point is so controversial and crucial, the citations are detailed below.

The degree to which bears are dispersed relative to one another varies directly with dispersal of preferred foods. Thus, despite the rarity of social groupings except for dams with their with their offspring, siblings, or mates (e.g., Mills 1919), bears commonly aggregate to feed at sites where food is especially abundant, particularly those hosting salmon spawning streams, carrion concentrations, patches of mast or fruit, or garbage dumps. Lewis & Clark observed aggregations of grizzlies along the Missouri River, for instance at fords where some bison had drowned when their herds crossed (cited by Mills 1919:32). Storer & Tevis (1955) reviewed reports on California grizzlies migrating to seasonal concentrations of mast, berries, and other foods; aggregations of up to 40 bears were documented. Martinka (1974:26) reports "large" groups of grizzlies in Glacier National Park, USA "on lowland meadows and snowslides in spring, subalpine areas in late summer, and along a non-native kokanee [red] salmon (Onchorhynchus nerka) spawning stream in fall." Pearson (1975) observed concentrations of grizzlies in berry patches in the southwestern Yukon territory. F. Craighead (1976, 1979) provides many examples of Yellowstone grizzlies aggregating at natural food sources, including berry patches, pinenut stands, clover fields, sedge seepages, streams where fish were spawning, and carrion. As many as 25 grizzlies were seen together feeding at a single ungulate carcass.

They also aggregated at garbage dumps; 135 were seen at a single dump during 1 exceptional night and 88 on another, although the average was far lower. (See also Judd & Knight 1980). As many as 13 grizzlies were found bedded within an area of several hundred meters in timbered retreats near feeding areas (F. Craighead 1976).

Aggregations of grizzly bears were also once a common sight the coasts of California. Oregon, and Washington, especially along streams hosting migrations of spawning salmon; such aggregations can still be seen in British Columbia and in Alaska. For example, concentrations of grizzlies have been reported on Kodiak Island in drainages for Karluk Lake (Troyer 1962; Troyer & Hensel 1964; Berns & Hensel 1972) as well as in alpine areas (Atwell et al. 1980). Similar reports are given for the Alaska Peninsula, for instance near Chignik and Black Lakes (Glenn & Miller 1980) and McNeil Falls. Each summer, up to 80 grizzlies feed on salmon at McNeil. Over 30 have been seen there simultaneously (Rausch 1968; Stonorov & Stokes 1972; Bledsoe 1975). Up to 20 grizzlies were seen feeding on sedge in a 40-acre tidal flat near McNeil River; several were seen eating a beached whale carcass (Egbert & Luque 1975; Egbert & Stokes 1976). Concentrations of grizzlies along shorelines to feed on vegetation and marine carrion were also reported by Wood (1976) and by Glenn & Miller (1980); but the authors did not state how many bears aggregated at the carrion.

Perry (1966) cites numerous cases where dozens, and in some cases nearly 100 polar bears gathered at carcasses of dead whales or walruses (some of which had been killed by humans). Perry also relates sightings of up to 29 polar bears adrift on a single ice floe. Andersen reported 56 polar bears at a single whale carcass in the Barents Sea (cited by Taylor et al., in press; see photo by Andersen in Costeau 1981:786-787).

Schorger (1949) reviews reports from the 1800's of Wisconsin black bears aggregating at food concentrations and of bears following bison herds. Garshelis & Pelton (1981) report aggregations in areas of the Great Smoky Mountains at sites where favored types of acorns (mast) are most abundant, in agreement with earlier reports by Harlow (1961) for eastern North America. Herrero (1983) reports aggregations of black bears in a roadside meadow in Yoho Park and at a garbage dump near the town of Jasper in Canada. Frame (1974) reported a similar aggregation of black bears during salmon runs at Olsen Creek in Alaska. Others have been reported in Washington, Oregon, and California. Coastal Washington black bears concentrate on tidelands during spring (Lindzey & Meslow 1977b). In Arkansas, T. Smith (pers. comm.) has seen black bears aggregate to catch fish trapped in pools left as lakes or rivers dried up.

J. Craighead & Mitchell (1982:530) state that

> These population concentration sites can be characterized as population activity centers or "ecocenters." They may best be visualized as ecological magnets that attract and hold high densities, not only of bears, but also of many other omnivorous species such as ravens, gulls, magpies, coyotes, and racoons.

Aside from amount and quality of the food obtained at dumps--which is thought to be highly nutritious for bears (e.g., Craighead et al. 1974; Rogers 1976, 1977)--dumps may be "unnatural" only in the high degree of reliability and long-duration each year that food was available at the same sites. Natural food concentrations tend to be more sporadic from year to year and more transient, such that there is probably more variation in which bears associate together. By contrast, stability in richness of a major garbage supply and particularly in its location, may lead to unusual stability in which bears aggregate and interact together at a feeding site, leading in turn to unusually stable social relationships (see Hornocker 1962; Stonorov & Stokes 1972; Egbert & Stokes 1976). Thus, although social relationships associated with feeding at dumps may differ in degree, there is no evidence that they differ in kind, from relationships associated with feeding at natural food concentrations.

Thus, one can dismiss the hypothesis that conditions prior to dump closure were too unnatural for YNP results to be applicable to other populations. A more heuristic approach is to view those conditions as an extreme on a scale of feeding aggregations--an extreme in both density of bears and in their familiarity with one another. This should affect magnitude of the parameters of each model, but not its basic form.

12:II.B. Naturalness of Mortality Patterns

Especially for subadult and adult males, prior to dump closure, mortality rates for Yellowstone grizzlies were probably more natural than for many other bear populations, particularly those south of Canada. As in the populations at Kluane Game Sanctuary in the southwestern Yukon (Pearson 1975), at McNeil (e.g., Glenn et al. 1976), and in other areas where bears are legally protected from harvest, YNP grizzlies apparently suffer less human-induced mortality than in all but the most isolated of the unprotected populations (e.g., Brooks Range, see Reynolds 1976, in press). Bunnell & Tait (1981) consider hunting to be the primary cause of mortality among adults not legally protected from harvest, as has been documented in at least 5 black bear populations (Lindzey et al. 1976; McCaffrey 1976; Rogers 1976, 1977, 1983; Graber 1981; Kohn 1982). Some Yellowstone grizzlies were killed by hunters, mainly on the periphery of the Park. A few were killed accidently by vehicles or died while being handled for research purposes. A number were killed outside or inside Yellowstone National Park to protect livestock, property, or people from the bears. Mortality data on YNP grizzlies has been presented by Craighead et al. (1974), F. Craighead (1979), J. Craighead (1980), Meagher (1978), and Schullery (1982); those data were summarized and discussed in Chapter 6 (Tables 3:3, p.31, and 6:5 p.183) ;that included discussion of how closure of the YNP dumps affected number of bears killed by humans over the next few years. In any event, known human-induced mortality seems to have accounted for no more than half the calculated attrition in YNP.

The question of how well results on Yellowstone bears apply to other populations cannot yet be answered with certainty--any more than one can assess _a priori_ the generality of findings from any other bear population. Certainly, results for Yellowstone grizzlies from 1959-70 were affected by the fact that the bears regularly aggregated to feed. Hence, results on YNP grizzlies are likely to have most applicability to other populations which form large feeding aggregations occur each year (e.g., at McNeil River). Conversely, they are likely to have less applicability to populations where the bears seldom aggregate to feed. Applicability would also depend upon other similarities and differences in population dispersion and density, as well as in habitat type, food type and abundance, climate, human influences, and other environmental factors. But one cannot yet quantify estimates for how great those similarities or differences might be. The most heuristic approach now would seem to lie in testing, not in assuming a priori, how similar or different other populations are.

One would expect the specific parameters (coefficients) of the mathematical models presented here to vary among populations and species, partly as a result of sampling errors, and partly as a result of differences in relative impacts on them by biosocial factors such as density/biomass of adults, and by environmental factors such as climate, food supply, pathogens, predators, and humans. For example, in populations where food is normally so abundant that variations in its abundance have negligible impact on reproduction and recruitment, biosocial factors and hunting might control fluctuations in population dynamics. By contrast, in populations where food supply is highly variable and famine common, density dependence might have comparatively little effect (e.g., Rogers 1976, 1977, 1983).

The models presented here should help to increase the efficiency of continuing research on YNP grizzlies and other bear populations--whether that research is aimed at direct management applications, or at refining or obtaining basic insights. For example, from a management perspective, they indicate that if rough estimates of food supply show it to be too high for estimation errors to have much effect on predictions for reproduction and recruitment, more precise estimates would be of little benefit. Conversely, if food supply appears to be in the range where reproduction and recruitment are most sensitive, precise assessment might be essential. Similarly, intensity of censusing of the bears themselves might be governed in part by results from preliminary censuses as to whether density/biomass of any age-sex class is in a critical range.

12:III. SUMMARY

1) Aggregations of grizzly bears at sites of food concentration are common in many habitats. Aggregations at Yellowstone dumps were not essentially different, just more extreme. They were extreme in mean and peak numbers of bears present. They were also extreme in stability of the food source in terms of its location and duration each year. So membership of bears encountering one another there might also have been more stable than is usual. That could have led to unusual stability and clarity of social relationships, including greater tolerance for proximity by conspecifics. Social strife, though high, might have been lower than is typical in other

aggregations of comparable density, but lesser familiarity. We do not know whether enhanced familiarity reduced components of social rituals (e.g., courtship) normally serving to establish familiarity, although that is likely. It might have also contributed to degree of promiscuity by females, particularly with large otherwise terrifying adult males.

2) Contrary to the viewpoint expressed by some critics, and in agreement with that of the Craighead research team, there does not seem to have been a distinct "dump sub-population" among Yellowstone grizzlies. Rather, there seems to have been a gradient in amount of dump usage by different bears, some visiting dumps daily throughout the summer, others seldom if ever visiting them. Because bears censused at dumps seem to constitute the majority (possibly over 90%) of YNP residents, census figures and analyses based thereupon are probably representative for YNP residents, but less so for bears whose activity centers were on the periphery of the Yellowstone Ecosystem. Rates of reproduction and recruitment for bears living on the periphery were presumably less influenced by fluctuations in garbage supply or by social strife in aggregations. But the nature and extent of these differences along the gradient of dump visitation cannot yet be quantified.

3) Applicability to other populations of these results, especially the general theoretical model (Chapter 13), should not be either accepted or rejected *a priori*, but tested by reference to data on other populations. Until this is done, one can only speculate in

general terms, for instance as follows: Results for Yellowstone grizzlies are probably most applicable to other grizzly populations where the bears regularly form dense feeding aggregations, such as that at McNeil Falls. By contrast, Yellowstone results are probably less applicable to grizzly populations (e.g., Kluane National Park) where such aggregations are rare, and even less so to other species. Nevertheless, the basic form of the models derived might be applicable to virtually any other population of bears and perhaps to populations of some other taxa. Indeed, some of their fundamental properties are similar to those of the conceptual model developed by Medin & Anderson (1979:Fig. 5).

CHAPTER 13

TOWARDS A THEORETICAL MODEL FOR THE DYNAMICS OF BEAR POPULATIONS

13:I. INTRODUCTION

In Chapter 5, parameters of reproduction and of recruitment between ages 0.5-5.5 years were regressed against indices for total food supply, supply per bear, and supply per unit bear mass. Supply per unit bear mass was the best predictor for virtually all of those parameters. The inference was made that this is because food supply per unit bear-mass is the index most closely correlated with nutrient-energy balance--because balance depends on amount of food needed, which can be approximated in terms of mass of food per unit mass of bear. In other words, that discussion assessed levels of reproduction and recruitment vs. food supply relative to food requirements--although it did not consider how that particular subdivision of the food was achieved.

Then, in Chapter 8, population biomass was shown to be a better predictor than population density for rates and levels of reproduction and recruitment; adult biomass was better still. Both sets of results provide evidence of negative density dependence--that reproduction and recruitment rates are impaired at high adult population density/biomass. Food competition is apparently only 1 of several means by which density dependent effects are exerted.

In this chapter, the first steps are taken towards deriving the theoretical mathematical models needed so that population dynamics can be realistically simulated as a function of both environmental and biosocial factors, according to the relationships revealed in previous chapters, including those summarized in Fig. 13:1.

That builds on the work of previous investigators, especially Medin & Anderson (1979: Fig. 5). They developed a largely schematic model representing productivity (#offspring/AdF/year) in mule deer as a sigmoidal function of both precipitation and population density. Productivity reaches its asymptotic maximum when precipitation is at its (observed) maximum and population density is zero (i.e., this represents only the negative feedback effects of density on productivity). That is fundamentally similar to the model developed here. But this model progresses further from the schematic to the mathematical and can be more thoroughly paramaterized from statistical models fit to empirical data, as shown in previous chapters. Other differences in the models are imposed by differences in the biology of mule deer vs. bears. For example, interbirth interval is usually 1 year in deer but 2-4 years in bears. Also, whereas productivity is represented as a negative-feedback function of _total population_ density for these mule deer (see also McCullough 1979), in bears it is mainly a function of _adult density_ particularly male adult density.

For purposes of this model, recall that recruitment to any age "a"--i.e., recruit density, cohort size at that age--is designated "#R_a. Because "a"=0 at birth, "#R_0" designates the total number of offspring born per year, neonate density or natality for the entire population. By contrast, natality _rate_ per whelping female, i.e.,

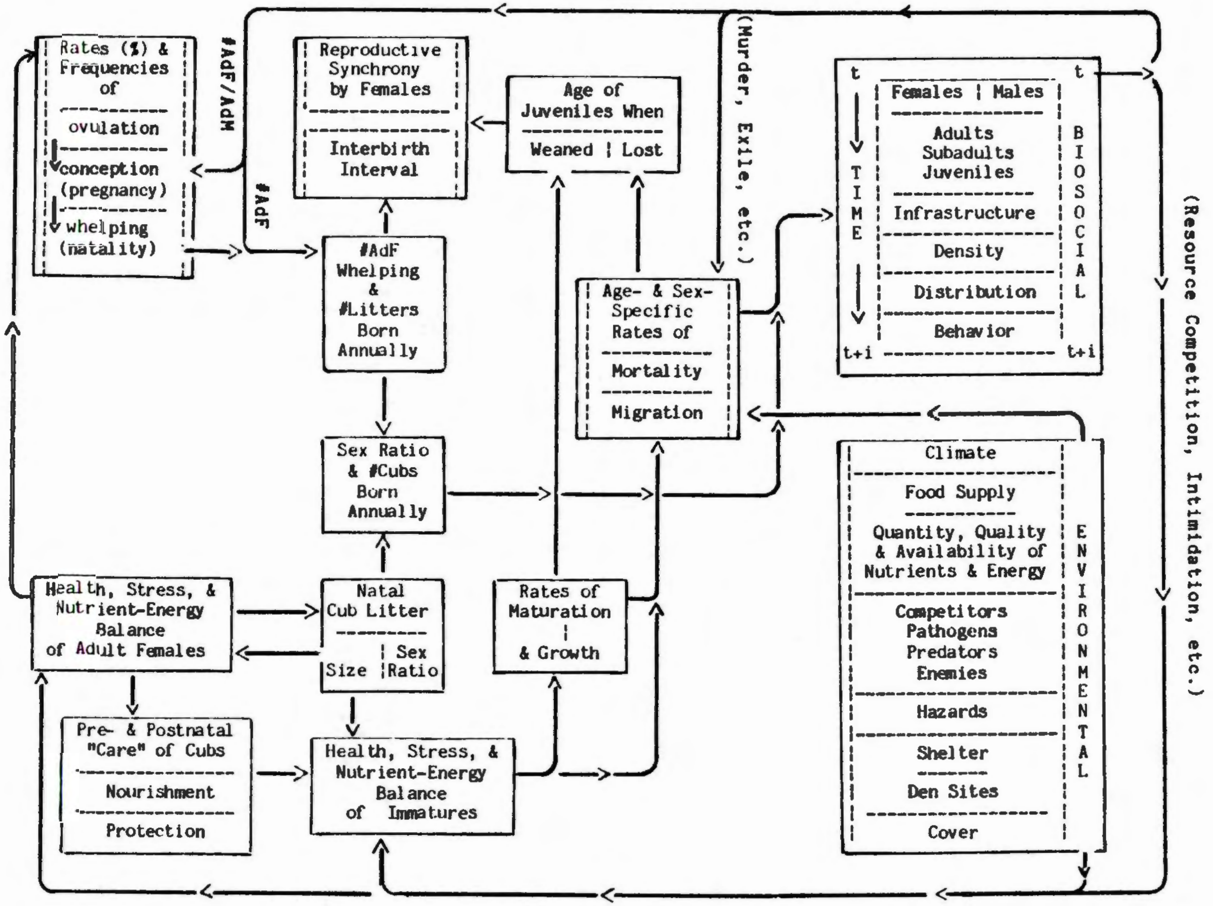

Fig. 13:1. Combined environmental and biosocial influences on reproduction, survival, and migration in a bear population.

number of neonates per dam and per litter, natal litter size, is designated by "$\#R_0/L$." Likewise, the mean number of offspring per natal litter reaching age "a" is "$\#R_a/L$." Natality per adult female $\#R_0/AdF$ differs from natality per dam or per litter $\#R_0/L$ in that "#L" represents only that fraction of the adult females that whelped in year t.

$$\#L = \#AdF * \#L/AdF$$

Findings presented in previous chapters indicate that most of the reproductive parameters examined vary as functions of both food supply and density/biomass. For example

$$\begin{aligned} \#L &= f_1(FS) \\ &= f_2(N) \\ &= f_3(FS/N) \end{aligned}$$

So in cases where any parameter is represented as a function of only food supply, or of only density, "=" is used to mean "tends to equal," i.e., "would be equal, were it not for perturbations by intervening influences," "all other factors being constant." Where other variables do intervene, their addition to the model should improve the accuracy and precision of predictions derived from it. Thus, each reproductive parameter (e.g., #L) can be written as function of food supply in one equation and as a function of population density in a second, even though it is potentially a function of both food supply and number of bears sharing that resource.

Recall that "0" FS represents not a total lack of food, but that level of supply below which reproduction apparently does not occur,

FS_{min}. In other words, $FS = FS' - FS_{min}$, where FS' is food supply on an absolute, complete scale where 0 represents a total lack of food.

In cases where the relationship between reproduction or survival vs. food supply is basically sigmoidal (Fig. 4:1, p.48), yet curvature at low values is negligible (below "A" in Fig. 4:1), usage of FS rather than FS' in models enables one to use an asymptotic function rather than a sigmoidal one (also see Medin & Anderson 1979:Fig.s 4, 5, 9, and 10).

13:I.A. Density Independence vs. Dependence

From a modeling standpoint, density dependent relationships are considered to be modify density independent relationships. Thus, models like those presented here typically include separate density independent and dependent components; they shall be identified where appropriate.

Density dependence is used here to mean that a per capita perameter of reproduction (e.g., natality rate, whelping rate, or litter size) or recruitment varies as a function of density (or biomass), being subject to either negative feedback (negative density dependence) or positive feedback (positive density dependence). The density independent component can be thought of as representing a norm. Negative density dependence lowers values below that norm; positive density dependence raises values above it. Absolute level of the norm can vary in response to environmental factors. For example, the density independent norm for whelping rate is directly related to food supply. That is,

$$\#L_I/AdF \quad = \quad f(FS)$$

The maximum density independent norm that could be achieved at optimum food supply under given conditions would be symbolized as

$$\#L_{I:max}/AdF \quad = \quad f(OE)$$

were OE = other environmental factors. <u>Note</u>: Whenever $\#L_{max}$ is given, the density independent rate is implied even though the "I" term of the subscript has been omitted.

Two common types of models employing these concepts are (1) logistic and (2) stock recruitment. Only stock-recruitment models are presented here. That is followed by discussion of plans for integrating those stock-recruitment models into a dynamic population model.

13:I.B. Ricker Stock-Recruitment Models

Stock-recruitment models deal with the relationship between stock density (N) when a cohort is produced vs. density of recruits within the cohort either then (e.g., at conception or birth) or at a subsequent time. "Stock" refers to either the entire population or to a specific subpopulation, usually the parents of the specified cohort.

In a Ricker stock-recruitment model, the density dependent (DD) component is a declining exponential that is multiplied against the rising linear density independent (DI) component.

Density Components: $\underline{\quad DI \quad}$ $\underline{\quad DD \quad}$

$$\#R_0 = (\#R_{0:I}/N)*N * (e^{-b*N})$$

This model can be altered to represent recruitment to ages past birth simply by substituting the appropriate "$\#R_a$" for "$\#R_0$." The stock-recruitment curves fit by to the Yellowstone data by Stringham (1983) and here have many similarities to Ricker models, but also crucial differences.

13:II. STOCK-RECRUITMENT MODELS FOR BEAR POPULATIONS

13:II.A. Food Supply per Bear and per unit Bear-Mass

Population density can potentially influence rates of natality and recruitment in various ways. One of these is competition for food. Development of the model is begun here in these terms, but will later be modified for incorporation of other density dependent effects. In typical stock-recruitment models, recruitment is solely a function of density. But possible effects of food competition are ignored. By contrast, in logistic-like models, food competition is approached by relating density to carrying capacity of the habitat. Here, it is instead approached in terms of food supply per capita or per unit bear-mass.

If total food supply were constant, average per capita supply (FS/N) would decline hyperbolically towards 0 as density increased (Fig. 13:2). The impact of adding or subtracting 1 more member of the population decreases as population density (N) increases; that is because the difference between $\underline{1/(N) \text{ vs. } 1/(N+1)}$ is inversely related

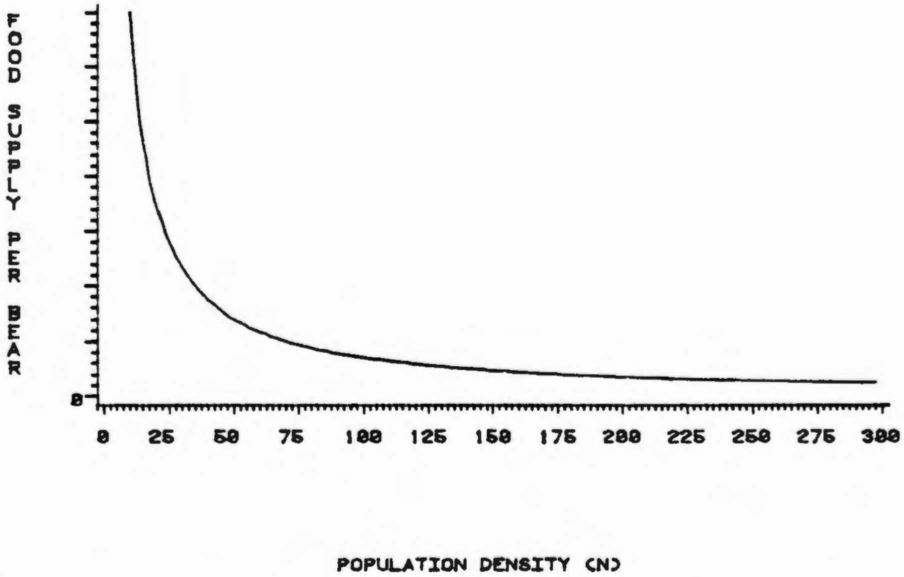

Fig. 13:2. Per capita food supply as a function of population density, where total supply is held constant in the model. Schematic.

to N. For example, if there were 2 bears equally sharing a given food resource, adding a third bear would reduce the share for each of the original animals by 1/6th (= 1/2 - 1/3). However, if there were initially 102 bears equally sharing that same resource, adding another would reduce the share for each of the original 102 bears by only about 1/10,500th (= 1/102 - 1/103). Note how slowly the curve drops towards the abcissa, reaching it at only very high density.

The strict hyperbolic shape of this relationship depends on a lack of correlation between food supply vs. concurrent density of the population or subpopulation (e.g., adults). Variation in food supply which is random relative to density would only produce scatter around the relationship for food supply per bear vs. density. But correlated variation in food supply could alter the shape of the relationship to some degree. The exact nature of this alteration has not yet been determined. In any event, _if_ rates of impregnation and whelping were governed solely through the effects of food supply per bear, then those relationships could be approximated with simple asymptotic functions (see Fig.s 5:1, p.94, and 5:2, p.98). The particular asymptotic function given below was chosen because it gave a good fit to data on Smoky Mountains black bears (Fig. 5:2, p.98) and for its simplicity, in lieu of any data requiring greater complexity.

$$\#L/AdF \quad = \quad [(\#L_{max}/AdF) * (1 - e^{-W*FS/N})]$$

where "L_{max}/AdF" is the asymptotic maximum _mean_ rate for impregnation (e.g., about 33% for bears with a mean interbirth interval of 3 years). Since whelping rate cannot exceed impregnation rate, or number of litters born exceed number conceived, #Lmax/AdF can also approximate the asymptote for whelping rate, and #Lmax the asymptote for whelping level. If density of adult females varied only randomly with respect to food supply, then density of neonate litters, whelping level, would also be an asymptotic function of food supply:

$$\#L \quad = \quad (\#AdF) * [(\#L_{max}/AdF) * (1 - e^{-w*FS/N})]$$

Thus, whelping rate and level could both be represented as families of asymptotic curves, each curve corresponding to a different density of adult females (Fig. 13:3).

Fig.s 8:2 (p.253) and 13:4 relate mean cub litter size to population density. Recall that size cannot fall below 1 C/L; for without at least 1 cub, there would be no litter. Nor, apparently, does mean litter size rise above about 3 C/L in any grizzly population.

Recall too that natality (neonate density) is the mathematical product of adult female density, their whelping rate, and mean size of their litters.

$$\#R_0 \quad = \quad (\#AdF) * (\#L/AdF) * (\#R_0/L)$$

If any of those 3 parameters is governed even in part by food supply per bear, then that would also be true for natality. For example, suppose that whelping level and litter size are both functions of food supply per bear (see Fig. 5:3, p.112):

If $\#R_0/L \;=\; u + v*FS/N$ within a given range of FS/N

then $\#R_0 = (\#AdF) * [(\#L_{max}/AdF) * (1 - e^{-w*FS/N})] * (C/L_{min} + v*FS/N)$ within that range of FS/N values.

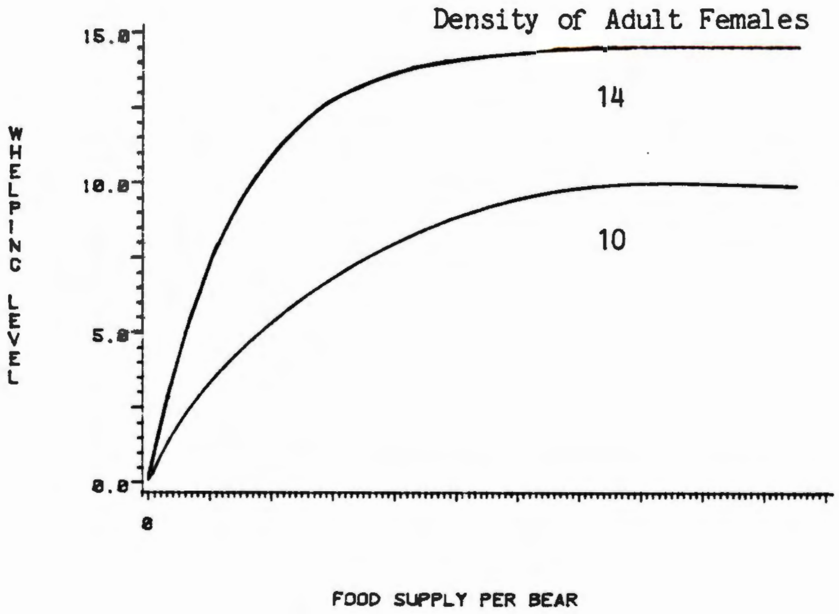

Fig. 13:3. Whelping level as a function of per capita food supply and density of adult females in the population. Each curve represents a different density of adult females. Schematic.

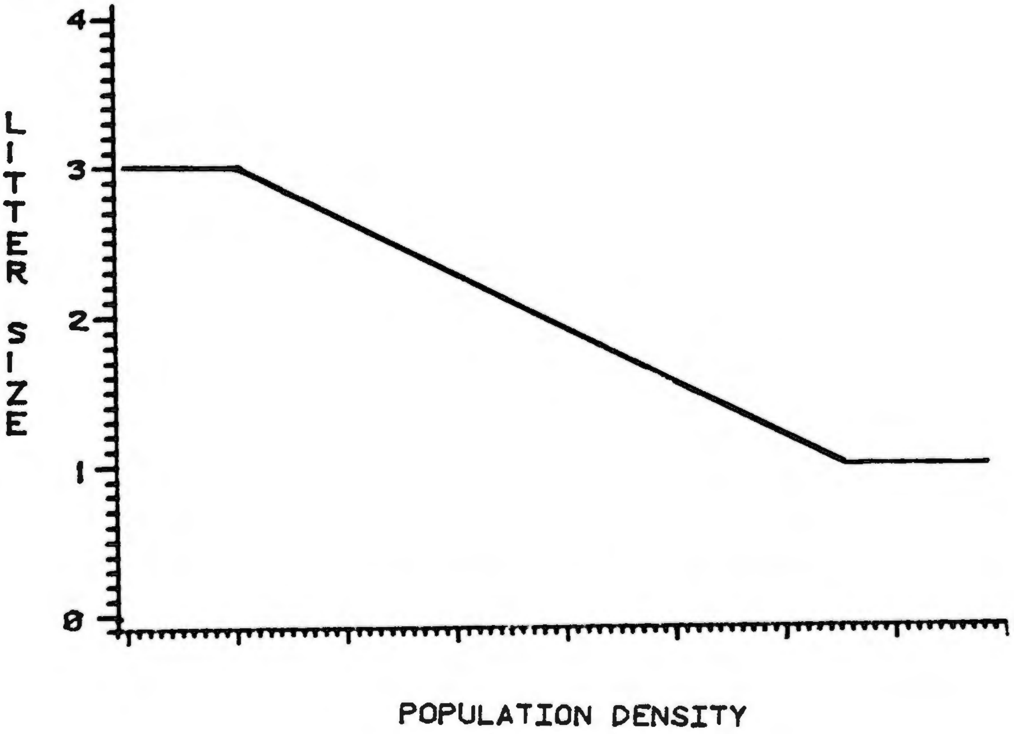

Fig. 13:4. Cub litter size as a function of population density. Schematic.

Now let us combine the terms for asymptotic whelping rate and litter size into a single term for the asymptotic ratio for numbers of neonates per adult female per year (productivity), where the asymptote is no longer a horizontal line (e.g., for $\#L_{max}/AdF$), but a rising straight line (Fig. 13:5)

$$\#R_{0:max} \;=\; (\#AdF) * (\#L_{max}/AdF) * (C/L_{min} + v*FS/N)$$

within the specified range for FS/N. Below or above that range, the term for litter size becomes C/L_{min} or C/L_{max}, respectively, where $C/L_{min} \geq 1$. Thus,

$$\#R_0 \;=\; (\#AdF) * [(\#R_{0:max}/AdF) * (1 - e^{-w*FS/N})]$$

In the above form, similarities and differences between this equation and a comparable Ricker model (shown below) become more apparent:

$$\#R_0 \;=\; (\#AdF) * [(\#R_{0:max}/AdF) * (e^{-b*N})]$$

In such a Ricker model, adult sex ratio is assumed to be the same at all levels of N and adequate to assure maximum rates of impregnation and parturition (whelping); N can be either density of just the adult subpopulation or of the whole population, according to what is most appropriate in each case.

In a Ricker model, the density dependent term "e^{-b*N}" has a value of "1" when N=0, and begins impairing natality/recruitment as soon as density rises above 0 (Fig. 13:6, plot A). By contrast, in the model presented here (schematically in Fig. 13:6, plots B and C), there is negligible density dependence for whelping rate so long as food supply per bear is adequate for whelping rate to be maximized. But once per capita food supply declines below some threshold, higher

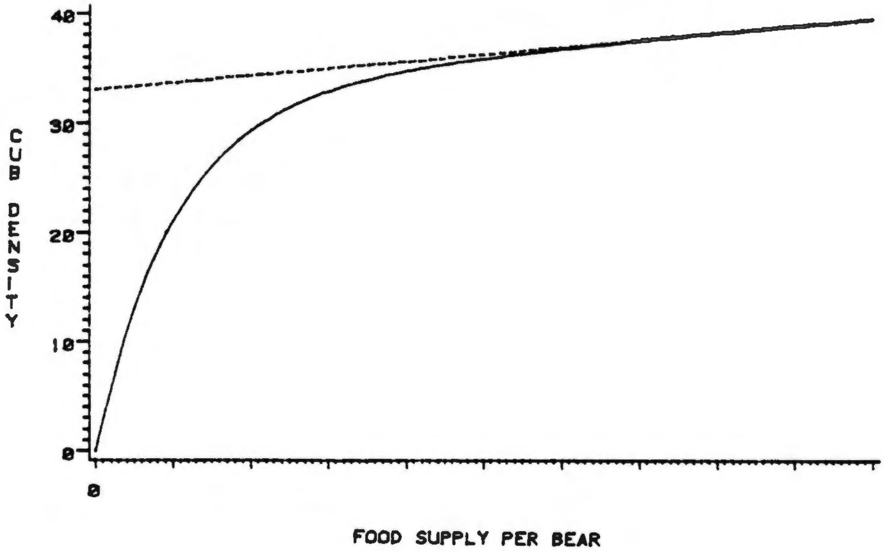

Fig. 13:5. Cub density (cohort size) as a function of per capita food supply. Schematic.

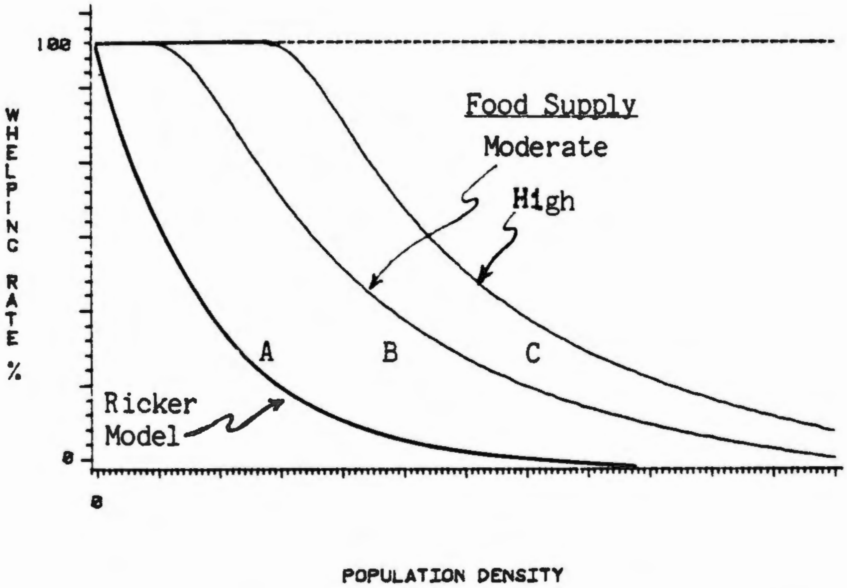

Fig. 13:6. Density dependent components for models of whelping rate. Schematic. Comparison between a Ricker model (A) based on population density alone, vs. a model based on per capita food supply at (B) moderate or (C) high levels of food supply, where food supply is held constant. Maximum whelping rate is assumed to be 100% of all _fertile_ females--which constitute only a fraction of all females in the population (e.g., about 33% for Yellowstone grizzlies).

population densities reduce whelping rate, first with increasing rapidity, then more slowly in a sigmoidal pattern. The larger the supply of food being shared by the bears, the higher total density must become before supply per bear becomes limiting--i.e., the higher the density at which whelping rate begins to decline below maximum (compare plots B vs. C in Fig. 13:6).

The curves given in Fig.s 13:7 - 13:10 are based on 2 simplifying assumptions: (1) Food supply is treated as being constant, so that all variation in food supply per bear is due to variation in population density. The constant value of food supply assumed (1500 units) approximates the observed mean for 1959-81. The term "unit" is applied because the index for natural food supply (and climate) was dimensionless, aside from being equated with a corresponding tonnage of garbage. (2) To more clearly reveal effects of just the negative density dependent term, density of adult females is also held constant at 44 adult females, the actual mean for 1959-70 in YNP. Because variation in adult female density was only ±4, ignoring that variation should have negligible effect on how well the model serves its schematic function here.

Curves for whelping level are similar to those for whelping rate, so long as density of adult females is not correlated with <u>concurrent</u> food supply per bear. But curves for densities of cubs and older recruits would differ, in part because they are products of cub litter size too, which is also a function of food supply per bear, and

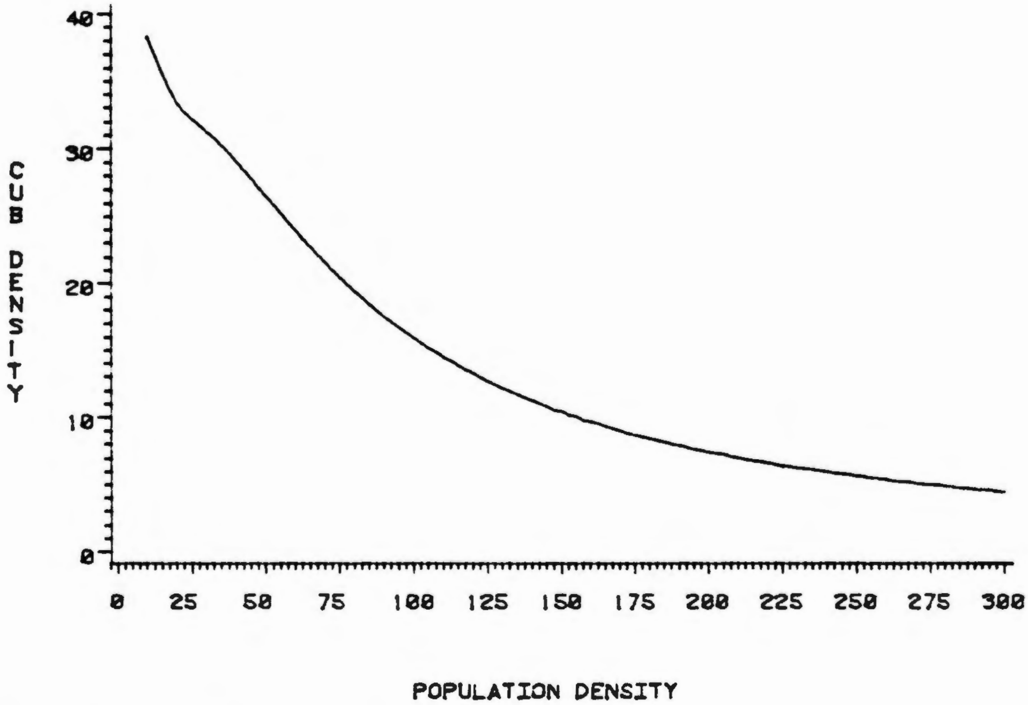

Fig. 13:7. Density dependent component for cub density as a function of population density, where food supply is held constant in the model.
Schematic.

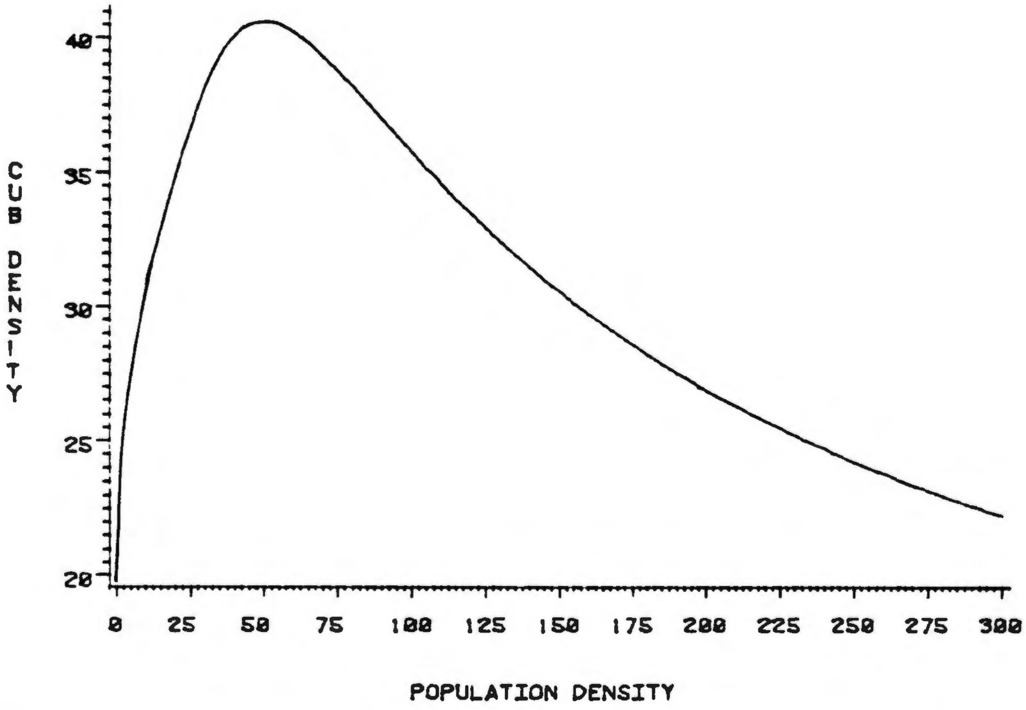

Fig. 13:8. Cub density as a function of population density, including both density independent and dependent components in the model, and where food supply and adult female density are held constant. Schematic.

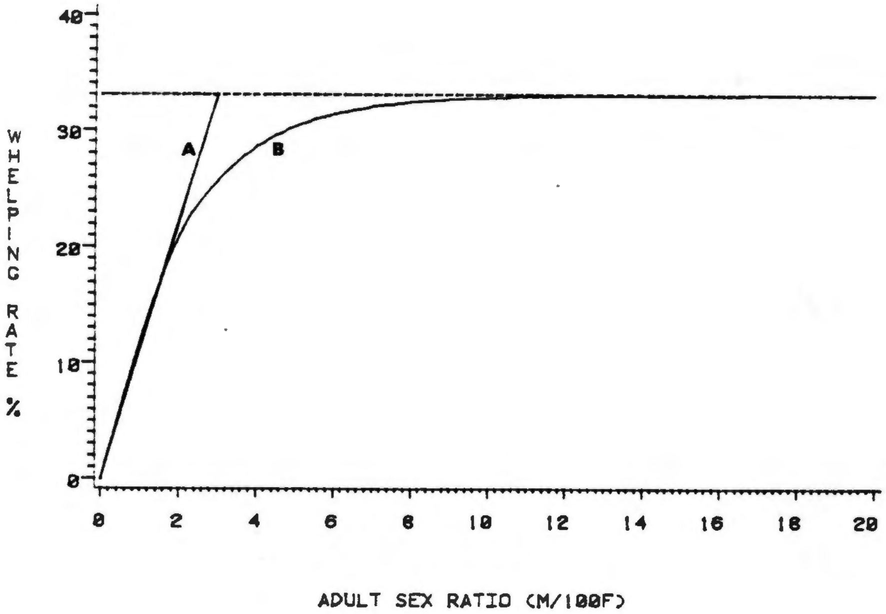

Fig. 13:9. Positive density dependent component of the relationship for whelping rate as a function of adult sex ratio. Schematic.

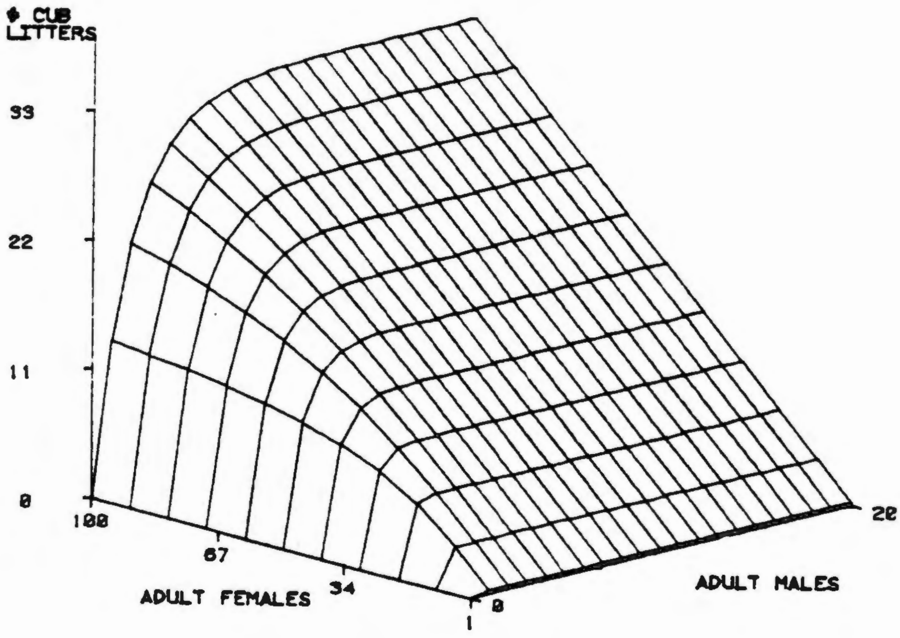

Fig. 13:10. Whelping level as a function of densities of adult females (density independent) and adult males (positive density dependent). When adult males are abundant enough for whelping rate to be maximized, whelping level (density of cub litters) is directly linearly related to density of adult females. Schematic.

has a different pattern of sensitivities than does whelping rate to changes in food supply per bear (Fig. 13:4, p.409). The density dependent curve for cub density vs. food supply per bear would not reach asymptote when whelping rate and level do, but would instead keep increasing until litter size also reaches its ceiling (compare Fig.s 13:4 vs. 13:6 vs. 13:7). Hence, when cub density is plotted vs. adult (population) density, the relationship does not necessarily show sigmosity at low adult (population) density; rather, the whole curve for this density dependent component approximates a simple declining exponential or semi-logarithmic curve (Fig. 13:7).

Consequently, when that density dependent component is included with the density independent components for a complete stock-recruitment model (whose form is superficially similar to that of a Ricker model), recruitment declines in a roughly semi-logarithmic fashion at moderate to high population densities (Fig. 13:8). That might explain, at least in part, why whelping rate and level, as well as cohort sizes, for Yellowstone grizzlies declined in approximately that same fashion while adult density/biomass increased (Fig.s 8:4-8:8, pp.259, 260, 262, and 265).

However, let it be noted that if the density dependent term is based on just per capita food supply, the curve does not drop to the abcissa quickly enough to be realistic. That probably reflects the need to take into account other sources of density dependence. As a first approximation of that, N is raised to an exponent "z" (FS/N^z). An exponent of 1.4 gave results that were close enough to the regression curves derived in Chapter 8 to serve the purposes of this schematic.

$$\#R_0 = [\#AdF * (\#L_{max}/AdF) * (1 - e^{-w*FS/N^z})] * (C/L_{min} + v*FS/N)$$

Note that the terms which are functions of food supply per bear constitute the density dependent components of the equation:

$$(1 - e^{-w*FS/N^z}) \text{ and } (C/L_{min} + v*FS/N)$$

The other terms constitute the density "independent" components.

$$\#AdF \quad \text{and} \quad \#L_{max}/AdF$$

Note that derivation of the model in terms of food supply per bear--an index of nutrient-energy balance that combines environmental and biosocial influences--enables one to avoid the greater complexity entailed if separate terms are used for food supply (or other environmental variables) and density--as in the model by Medin & Anderson (1979:Fig. 5) which represents productivity as a function of both precipitation and population density. Related to that is the fact that precipitation was used as an index for body fat reserves of the deer, and thus as an index of nutrient-energy balance which ignored the effects of density on nutrient-energy balance.

Without data for Yellowstone grizzlies on whelping rate and density/biomass past 1970, one can make only rough approximations of the asymptotic relationship between whelping rate vs. food supply per bear and per unit bear mass over the full range of food supply levels observed during 1959-81. Indeed, much remains to be done before these theoretical models are thoroughly fit (parameterized) to the Yellowstone data. So far, only a few preliminary steps have been taken, in order to illustrate the models and to demonstrate their relevance to the Yellowstone data.

13:II.B. Density of Adult Males and Adult Sex Ratio

The version of the models for whelping rate and level, as well as recruit densities, given in the previous section all tacitly assumed that density of adult males was adequate for rates of impregnation and thus whelping to reach the maximum level permitted by nutrient-energy balance of the females. Now let us consider how one might incorporate effects of adult sex ratios so low that rates of impregnation and whelping can't be maximized. For simplicity, modeling is begun for cases where food supply per bear is not limiting, and the term representing food supply per bear is reintroduced later.

In bears, adult males seem to contribute to reproduction only by siring offspring. So, once there are enough adult males present to impregnate all estrus females, further increase in relative abundance of adult males would not further increase reproductive rate. This relationship would approach the maximum impregnation rate linearly if all adult males sired an equal maximum number of litters (Fig. 13:9, plot A). By contrast, if only some (e.g., dominant) males sire the maximum number of litters and mean siring rate per male declines as density of adult males increases, then the ceiling of 100% impregnation of estrus females might be approached more-or-less asymptotically (Fig. 13:9, plot B; see Allen 1981: Fig.3).

$$\#L/AdF = [(\#L_{max}/AdF) * (1 - e^{-x*s*\#AdM/AdF})]$$

where "s" is mean siring rate, number of females impregnated and litters sired per adult male (#L/AdM); "x" is a coefficient used to scale siring rate for the equation. Siring rate determines how steeply the asymptote is approached. This particular form of asymptotic function was chosen abritrarily for simplicity, in lieu of data requiring a more complex form.

Maximizing rates of impregnation and whelping depends on achieving at least some minimum adult sex ratio. Hence, the density of adult males needed for maximizing those rates is directly related to the density of adult females. That is illustrated by the simulated 3-dimensional plot in Fig. 13:10. When adult males are abundant enough to maximize rates of impregnation and whelping, densities of cub litters and of cubs can also be maximized, for the relationships between densities of cub litters and of cubs vs. density of adult females are linear. But when adult males are scarce, these latter relationships are curvilinear. Neonate density would be calculated as shown below:

$$\begin{aligned}\#R_0 &= [\#L] * (\#R_0/L)\\ &= [\#AdF * (\#L_{max}/AdF) * (1 - e^{-x*s*\#AdM/AdF})] * (\#R_0/L)\end{aligned}$$

13:II.C. Models Encompassing Food Supply, Population Density, and Adult Sex Ratio

To complete the models, let us now reintroduce the terms representing effects of food supply per bear:

$$\#R_0 = [\#AdF * (\#L_{max}/AdF) * (1 - e^{-x*s*\#AdM/AdF}) * (1 - e^{-w*FS/N^z})] * (C/L_{min} + v*FS/N)$$

where

$$\#L/AdF = [(\#L_{max}/AdF) * (1 - e^{-x*s*\#AdM/AdF}) * (1 - e^{-w*FS/N^z})]$$

$$\#R_0/L = (C/L_{min} + v*FS/N)$$

Equations for cohort sizes at older ages ($\#R_a$) would be similar, except that attrition since birth of whole litters and of cubs from within litters (litter size) would necessitate corresponding alterations of the terms "$\#L_{max}$" and "$C/L_{min} + v*FS/N$," respectively. Incorporation of those terms shall be necessary for development of these stock-recruitment models into a population model. Replacement of the density term (N) with biomass (BM) should further increase its realism.

13:III. TOWARDS A DYNAMIC POPULATION MODEL

So far, these models have been given only in general form, potentially applicable to any population of bears and perhaps of some other taxa. The next step in development of a simulation model shall be to fit these models, as well as possible, to the Yellowstone data (i.e., to paramaterize them). Then the recruitment component for each age needs to be organized in sequence so that they can be incorporated into a dynamic population model. One potentially applicable approach is use of a projection matrix like that developed by Wu & Botkin (1980). Other relationships needed for that matrix, such as interbirth interval relative to food supply and density/biomass and age-dependent changes in fecundity have also be derived (see Chapter 5:II.B.2; Stringham, in prep). An alternative approach would be a simulation model of the sort developed by Medin & Anderson (1979:Fig.5).

Plans for continuing this project include (a) completing development of the dynamic simulation model, as a basis for (b) studying its fundamental mathematical properties (in collaboration with a mathematician), (c) examining the effects of various scenarios of changes in food supply and population density or infrastructure (e.g., as a consequence of human-induced changes in habitat or in the population), and finally for (d) determining the implications of the model for life-history strategies of bears. This should be accompanied or followed by fieldwork to test and extend the resultant insights.

13:IV. SUMMARY

1) Stock-recruitment models typically relate size of each cohort at a specified age to density of the population or of the parental subpopulation when the cohort was produced--for instance at conception, birth, or first censusing.

2) The theoretical stock-recruitment model developed here for bear populations is Ricker-like in several respects: (a) It is mainly cohort-specific. (b) The density dependent term is multiplied against the density independent term, rather than subtracted from it as in a logistic-like model. In other respects, it is more similar to a

logistic-like model, for instance in relating density to an index of environmental conditions. However, it also has importance differences from both Ricker and logistic models.

2a) In a Ricker model, density dependence is based on density per se, whereas in a logistic model it is based on density relative to habitat carrying capacity. Here it is based on density relative to food supply, for instance in terms of food supply per bear or per unit bear mass.

2b) Accordingly, whereas density dependent impacts begin at even the lowest densities in typical Ricker and logistic models, in this they begin only after food supply per bear or per unit bear mass falls below some threshold.

2c) A Ricker or a logistic model assumes that adult sex ratio is always high enough for rates of fertilization and "whelping" to be maximized in lieu of density dependent impairment. By contrast, the present model allows for effects of lower adult sex ratios.

2d) It is also intended that this model should represent differing intensities of per capita density dependent impact by adult males vs. adult females vs. other age-sex classes.

3) It is intended that in the near future, development of this theoretical static stock-recruitment model into a dynamic population model shall be (a) completed, (b) parameterized with data on Yellowstone grizzlies and/or other populations, and (c) incorporated into a complex projection matrix like that developed by Wu & Botkin (1980) or a model like that by Medin & Anderson (1979), so that

simulations can be run. Those simulations are intended to enhance ongoing management and field research of bears, as well as study of general theoretical phenomena such as life history strategies.

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APPENDIXES

APPENDIX A

KEY TO ABBREVIATIONS AND SYMBOLS

*	Multiplication (e.g., 2*3 = 6).
#	Number (e.g., #Ad).
%	Percent
a	Age (years)
A-A	Arithmetic relationship (e.g., Y = a + b*X).
A-L	Semi-logarithmic relationship (Y = a + b*lnX).
Ad, AdM, AdF	Adult, adult male, adult female
%AdM, %AdF, %C	Percents of adult males and females and of cubs in the population (e.g., %C = #C/pop. size).
AFW	Age at first whelping (birth of first litter)
AOFBC	All other factors being constant (all other things being equal).
AP	Age at puberty (i.e., onset of reproductive capability).
AW	Age at weaning (i.e., age when a litter is weaned, usually as yearlings in black bears) AW = BWI.
BWI	Birth to weaning interval = AW. This is the first part of the IBI.
C	Cub(s), average age about 0.5 years for most populations.
C/L	Mean size of cub litters in the cohort.
CL	Confidence level
e	Exponent base "e", i.e., "natural exponent".
f(N)	Mathematical function of "N" (density).
Fc	Per capita fecundity = (%FC*Pr)
fc	Total population fecundity (= FC * #AdF)
%FC	Percent female cubs

G	Generation length = AFW
GS	Garbage supply.
i	ith item.
IBI	Interbirth interval
#L	Number of cub litters in cohort born in year t.
#L/AdF	Whelping rate, proportion of females whelping.
ln(#Ad)	Natural log of number (density) of adults.
%M	Sex ratio, percent males (%M = #M/[#M+F])
%MAd, %MsAd, %MC	Percents of males among adults, subadults, and cubs.
n	Sample size
N	Population size or North, depending on context.
NFS	Natural food supply index (based on Picton's index of winter severity; see Table 4:5).
P:1t, P:2t	1- and 2-tailed significance levels (probabilities that the non-null hypothesis is false).
PFWI	Puberty to first whelping interval.
Pr	Productivity = C/L/IBI
r	Pearson product-moment correlation coefficient.
r^2	Coefficient of determination for regression or correlation.
R_a	Recruitment to (cohort size at) age "a" or time "t".
$\%R_{a--a+1}$	Proportion of cohort members at age "a" still present in the habitat or population at age "a+1".
RVI	Reproductive vigor index.

sAd	Subadult
t, t+1	Specified point in time (t) and 1 year later (t+1).
$\#C_t$	Number of cubs, i.e., cohort size at age 0.5 year during year t = $R_{0.5}$.
TFS	Total food supply = NFS + GS.
w/, w/o	With, without
WNBI	Weaning to next birth interval.
X^2	Chi-square statistic for significance tests.
X	An "independent = causal = controlling variable.
X ±SD	Mean for X, plus or minus standard deviation.
Y	A "dependent" or response variable.
YNP	Yellowstone National Park

APPENDIX B

ESTIMATING DENSITY OF 5-YEAR-OLDS IN YELLOWSTONE NATIONAL PARK

Recruitment to adulthood is due to both maturation of new 5-year-olds and immigration by adults, whether they are new to the area or are returning after an absence of 1 or more years. Reliable information is <u>not</u> available on the proportions of recruitment from age 4.5 to 5.5 years due to survivorship vs. immigration, or on the proportions of attrition due to mortality vs. emigration. Nor is it certain what proportion documented mortalities (Table 3:3, p.31) constitute of total mortalities.

Adult density decreased between consecutive years for only 4 of the 11 year-pairs (e.g., 1963 to 1964; Tables B:1 and B:2). In those 4 cases, documented mortalities of knwon and suspected adults (total 30) accounted for only 51% of change in adult density (total 59) between years t to t+1. If any mortalities escaped documentation, the full proportion of attrition due to death could have been underestimated. Conversely, if any recruitment also occurred between those 4 year-pairs, that would have masked an equivalent number of mortalities; so documented mortalities would constitute an even smaller proportion of total attrition.

Given those uncertainties about relative amounts of mortality vs. emigration, errors are assumed to have occurred in estimating density of 5-year-olds in each cohort. (Cases where the index for density of 5-year-olds is negative are those where there was such excessively high attrition of adults that it completely masked recruitment by 5-year-olds.) But it is hoped, and results interpreted accordingly, that the estimates for density of 5-year-olds were

Table B:1. Estimates for densities of total 5-year-olds and male 5-year-olds during 1959-70 among Yellowstone grizzlies.

Year t	Density of Adults in Year t	Change in Density Year t to Year t+1	+	Known Deaths in Year t	=	Estimated Density of 5-Year-olds in Year t+1	Year t+1
TOTAL							
1959	88	+14		7		+21	1960
1960	102	-23		9		-14	1961
1961	79	-20		3		-17	1962
1962	59	+13		5		+18	1963
1963	72	+10		5		+15	1964
1964	82	-12		4		-8	1965
1965	70	+2		5		+7	1966
1966	72	0		1		+1	1967
1967	72	+18		7		+25	1968
1968	90	+8		12		+20	1969
1969	98	-4		14		+10	1970
1970	94	--		23		--	1971
MALES							
1959	43	+12		5		+17	1960
1960	55	-20		3		-17	1961
1961	35	-17		1		-16	1962
1962	18	+11		1		+12	1963
1963	29	+5		2		+7	1964
1964	34	-7		3		-4	1965
1965	27	+2		2		+4	1966
1966	29	+2		1		+3	1967
1967	31	+13		2		+15	1968
1968	44	+9		9		+18	1969
1969	53	-4		8		+4	1970
1970	49	--		10		--	1971

* Data from Tables 3:3 and 3:6, based on J. Craighead et al. (1974).

Table B:2. Estimates for densities of female 5-year-olds during 1959-70 among Yellowstone grizzlies.

Year t+1	Total 5-Year-Olds	-	Male 5-Year-Olds	=	Female 5-Year-Olds
1960	+21		+17		+7
1961	-14		-17		+3
1962	-17		-16		-1
1963	+18		+12		+6
1964	+15		+7		+8
1965	-8		-4		-4
1966	+7		+4		+3
1967	+1		+3		-2
1968	+25		+15		+10
1969	+20		+18		+2
1970	+10		+4		+6

affected randomly, not systematically, by the errors. If so, then the errors in the exact values obtained may not distort the <u>relative</u> values, and corresponding correlations, although they could erroneously raise or lower regression plots.

Proceeding then with calculations for density of 5-year-olds:

$$\#\text{5-year-olds}_{t+5} = [\#\text{Ad}_{t+5} - \#\text{Ad}_{t+4} + (\#\text{Ad dying}_{t+4 \text{ to } t+5})]$$

For example, given that (a) there were 10 more adults censused in 1964 than in 1963, and (b) at least 5 adults died in 1963, then there must have been at least 15 5-year-olds in 1964--ignoring possible sampling errors. Mortality between each pair of years t+4 to t+5 was estimated by using the figure for documented mortalities of known adults in t+4 given by J. Craighead et al. (1974; reproduced here in Table 3:3, p.31). Density of male 5-year-olds was calculated in that same way (Table B:1). Then density of female 5-year-olds was calculated by subtraction of males from total 5-year-olds (Table B:2). Note that when McCullough (1981) estimated densities of 5-year-olds for this population, only the change in adult density from year to year was considered; no correction was made for known mortalities.

APPENDIX C

REPRODUCTIVE VIGOR INDEX

The reproductive vigor index (RVI) is used to estimate the net impact of all reproductive parameters on population growth rate. It is used to reveal how differences in reproductive rate among populations would affect their growth rates if that were the only differences affecting growth rate. It is not intended as an estimation of actual growth rates--rates which are also subject to those other influences ignored here, including differences in recruitment rates.

The reproductive vigor index is calculated through use of a Leslie projection matrix, as though one were calculating the density independent rate of population growth at stable age distribution for each of the populations considered. That rate is represented by the dominant eigenvalue of the matrix; the corresponding eigenvector represents the stable age distribution itself. Age distributions in these populations may never stabilize, due in part to (a) effects of a fluctuating environment on rates of reproduction, survival, and migration, and possibly to (b) density dependent feedback on those rates. Nevertheless, the reproductive vigor index provides a basis for estimating how population differences in reproductive rate would tend to affect relative growth rates for those populations, all other factors being constant.

The Leslie projection matrix is shown in Fig. C:1. All rows except Row 1 give rates of recruitment from age a to a+1 (R_a). By contrast, Row 1 gives <u>net</u> fecundity <u>rate</u> (fc_a), the <u>mean</u> number of daughters produced in year t+1 by females impregnated during year t at

$$\begin{array}{c|ccccccccccc|c|c|c|c|}
 & \multicolumn{11}{c}{\text{Age of Females (years)}} & & \#F & & \#F \\
 & 0 & 1 & 2 & 3 & \dots & G-1 & G & G+1 & \dots & A-1 & A & & t & & t+1 \\
\hline
\text{Age} & fc_0 & fc_1 & fc_2 & fc_3 & \dots & fc_{G-1} & fc_G & fc_{G+1} & \dots & fc_{A-1} & fc_A & & \#F_0 & & \#F_0 \\
0 & \%R_0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & & \#F_1 & & \#F_1 \\
1 & 0 & \%R_1 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & & \#F_2 & & \#F_2 \\
2 & 0 & 0 & \%R_2 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & & \#F_3 & & \#F_3 \\
3 & 0 & 0 & 0 & \%R_3 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & & \#F_4 & & \#F_4 \\
\cdot\cdot & \dots & & & & & & & & & & & * & \dots & = & \dots \\
G-1 & 0 & 0 & 0 & 0 & \dots & \%R_{G-1} & 0 & 0 & \dots & 0 & 0 & & \#F_{G-1} & & \#F_{G-1} \\
G & 0 & 0 & 0 & 0 & \dots & 0 & \%R_G & 0 & \dots & 0 & 0 & & \#F_G & & \#F_G \\
G+1 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & \%R_{G+1} & \dots & 0 & 0 & & \#F_{G+1} & & \#F_{G+1} \\
\cdot\cdot & \dots & & & & & & & & & & & & \dots & & \dots \\
A-1 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & \%R_{A-1} & 0 & & \#F_{A-1} & & \#F_{A-1} \\
A & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & \%R_A & & \#F_A & & \#F_A \\
\hline
\end{array}$$

Fig. C:1. Leslie projection matrix for exponential population growth, post-multiplied by the column vector for female infrastructure [density of females in each age class (0 for cubs to A for maximum reproductive age)] in year t, yielding female infrastructure for year t+1. (Symbols defined in text and Appendix Table A:1).

age a. Net fecundity _rate_ is calculated by multiplying percentage recruitment rate for all females between ages a to a+1 (years t to t+1) by their per capita fecundity rate--i.e., _mean_ number of daughters produced _per dam_--at age a+1 (year t+1):

$$fc_a = R_a * Fc_{a+1}$$

Thus, net fecundity _level_ in year t+1 for females of age a+1, equals number of females of age a in year t ($\#F_t$), multiplied by their recruitment rate to age a+1, multiplied by their per capita fecundity rate. For example, if there are 100 females of age a in year t, and 50% of them are recruited to age a+1, and each survivor produces 2 daughters, then on average, each of the 100 females of age a in year t contributes 1 daughter in year t+1. Note that since G represents generation length, age at first whelping, G-1 represents the age at first "successful" conception; so

$$f_a = 0 \quad \text{for all} \quad a < (G-1).$$

A is the oldest age at which females reproduce; survivorship past age A is also assumed to be negligible, both because that agrees with empirical data (see J. Craighead et al. 1969 and review by Stringham, in prep.), and to preserve critical mathematical properties of the matrix. The $\#F_t$ column vector presents size of each age-class at time t. Post multiplication of the Leslie projection matrix (L) by population size at t yields estimates for population size at t+1:

$$L * \#F_t = \#F_{t+1}$$

As described in the text, per capita fecundity is defined as the mean number of daughters per year per (adult) female:

$$(Fc) = (C/L/IBI) * (\%FC)$$

where %FC is percent of the cubs that were female. Productivity was assumed to be age-dependent, in according with the findings by J. Craighead et al. (1976), Alt (1982), and others (see review by Stringham, in prep.). Age-dependent changes in litter size were calculated by Stringham (in prep.). For example, to estimate mean size of litters produced by females of each age among Yellowstone grizzlies:

$$C/L_a = \frac{\underline{\text{(Mean C/L for YNP grizzlies)}}}{\text{(Mean C/L for all populations)}} * (1.10 + 0.18*a - 0.0064*a^2)$$

where the parabolic equation represents the age-dependent change in mean litter size averaged across 4 populations for which adequate data were available. Division of litter size for each population by mean size across all 4 populations, adjusts for differences in mean litter sizes among populations, and thus yields an age-specific curve appropriate to each individual population.

Although interbirth interval also seems to change with age or parity of a female, data were not sufficient for calculating a regression for that. So no compensation could be made for effects of parity or age on interbirth interval. In other words, the only age-dependent changes in fecundity used were those based on litter size.

Let it be emphasized that the same cub sex ratio of 45.5% females was used for all grizzly populations, since actual figures were available from too few of them to incorporate that as a variable, rather than as a constant, in the calculations. That figure of 45.5%

was obtained from data on more than 2,000 wild- and captive-born cubs (see review by Stringham, in prep.).

Age-specific recruitment rates were based on the recruitment schedule for female grizzlies in Yellowstone National Park derived by J. Craighead et al. (1974: Table 9). (Although those authors described it as a survivorship schedule, the possibility of not being able to distinguish some emigration from mortality, led me to use the term recruitment instead). This schedule is given in Table C:1. The recruitment schedule presented by J. Craighead et al. (1974) was calculated from average size of each age-sex class during the 9-year period 1959-67, thus excluding years when age-structure could have been seriously modified by the increased level of hunter kills in 1967 or by dump closure in following years (Chapter 4:III.C).

Although J. Craighead et al. (1974) argue that the population was growing exponentially (in an apparently density-independent fashion, with a stable age distribution) during that period, they did not correct differences in average size of age-classes between successive years to compensate for population growth. For example, suppose that:

> every age-class in a population were growing at a rate of +10%/year. Then, if there were 20 cubs and 10 yearlings in year t, there should be 22 cubs and 11 yearlings in year t+1. So recruitment rate between years t to t+1 for cubs would be 11/20 = 55%, not 10/20 = 50%.

Table C:1. Life table for female Yellowstone grizzlies.

Age (Years) a	Initial Age Distribution $\%L_a$	Recruitment Rate $\%R_a$	Fecundity = $(Ra)^*(Fc_{a+1})$ f_a
0.5	16.32	0.800 or 0.630	0.000
1.5	10.28	0.953	0.000
2.5	9.79	0.679	0.000
3.5	6.65	0.909	0.000
4.5	6.05	0.820	0.000
5.5	4.96	0.976	0.280
6.5	4.84	0.950	0.286
7.5	4.59	0.974	0.305
8.5	4.47	0.973	0.315
9.5	4.35	0.944	0.314
10.5	4.11	0.971	0.329
11.5	3.99	0.939	0.323
12.5	3.75	0.903	0.313
13.5	3.39	0.857	0.298
14.5	2.90	0.792	0.275
15.5	2.30	0.737	0.254
16.5	1.69	0.857	0.291
17.5	1.45	0.750	0.250
18.5	1.09	0.889	0.289
19.5	0.97	0.750	0.236
20.5	0.73	0.667	0.202
21.5	0.48	0.750	0.216
22.5	0.36	0.667	0.182
23.5	0.24	0.500	0.127
24.5	0.12	0.500	0.118

* The recruitment schedule is from J. Craighead et al. (1974: Table 9). Fecundity was calculated according to the equation for age-dependent changes in size of litter produced by females given earlier in this appendix.

The assumptions of (a) density-independent exponential growth rate and (b) stable age distribution, were discussed in Chapter 11. But those considerations aside, the recruitment schedule given by J. Craighead et al. (1974: Table 9) was deemed adequate as a basis for calculating the reproductive vigor index. A different recruitment schedule or population-specific sex ratio would have produced different index values. But the *relative* values for each population would probably not be seriously altered. Due to the expense involved, a variety of possible recruitment schedules could not be tested. But a difference in cub sex ratios was tested. The correlation found between RVI values obtained with 45.5% vs. 50.0% female cubs is 0.998.

VITA

Stephen Frederick Stringham was born in Denver, Colorado on 30 March, 1946. He is the son of Robert R. Stringham, an industrial chemist and patent agent, and of Joyce B. Stringham, an artist and who is active in Christian ministry. Stephen Stringham graduated from high school in 1964 and subsequently attended Diablo Valley College (Pleasant Hill, CA) and Humboldt State University (Arcata, CA) for undergraduate work in marine ecology and philosophy of science, graduating in 1969 with a B.Sc. degree in Biological Oceanography. From 1970-73, he attended the University of Alaska (Fairbanks), graduating in 1974 with a M.Sc. in Wildlife Management. That was followed by doctoral work in ecology at Texas A & M University (1976-78; College Station) and at The University of Tennessee (1979-1984; Knoxville).

Intermittent with scholastic work, Mr. Stringham obtained a variety of experience in various facets of ecology and environmental impacts, at educational institutions, private industry, and governmental agencies. As an undergraguate, Mr. Stringham held several positions as a lab or field assistant at Diablo Valley College, Humboldt State University, Dow Chemical Co., the U. S. Forest Service, and the U. S. Geological Survey. Other temporary jobs were held in construction, ranching, sales, and commercial fishing. As a Masters student, he worked for the U. S. Fish & Wildlife Service and in cooperation with the Alaska Department of Fish & Game, studying the behavioral ecology of moose. That was followed by 2 years in Austria for the World Wildlife Fund studying behavioral ecology of chamois and deer. As an undergraduate, Mr. Stringham served as a teaching assistant for courses in general biology, physiology, and anatomy. As a graduate student he served as a teaching assistant for courses in general biology, general ecology, mammalogy, and ethology; he also taught general ecology and physiology as an Instructor, at The University of Tennessee and Maryville College, respectively.

Mr. Stringham's research with Alaskan moose focused on mother-offspring relations, communication, and behavioral ontogeny, and he later did similar work with black bears in Alaska and Tennessee. However, the focus of his work during recent years has been the roles of adult males in populations of ungulates and carnivores. Future plans include continuation of those lines of research, with particular interest in the role of learning and other forms of behavioral versatility for adapting animals to their natural and human-altered environments. He is also interested in developing applications of "art," including the newest forms of computer animation, to enhance scientific research on wildlife behavior and ecology.

Mr. Stringham is a member of the International Association for Bear Research and Management, The Wildlife Society, and the Animal Behavior Society.