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A Population Analysis of the Yellowstone Grizzly Bears

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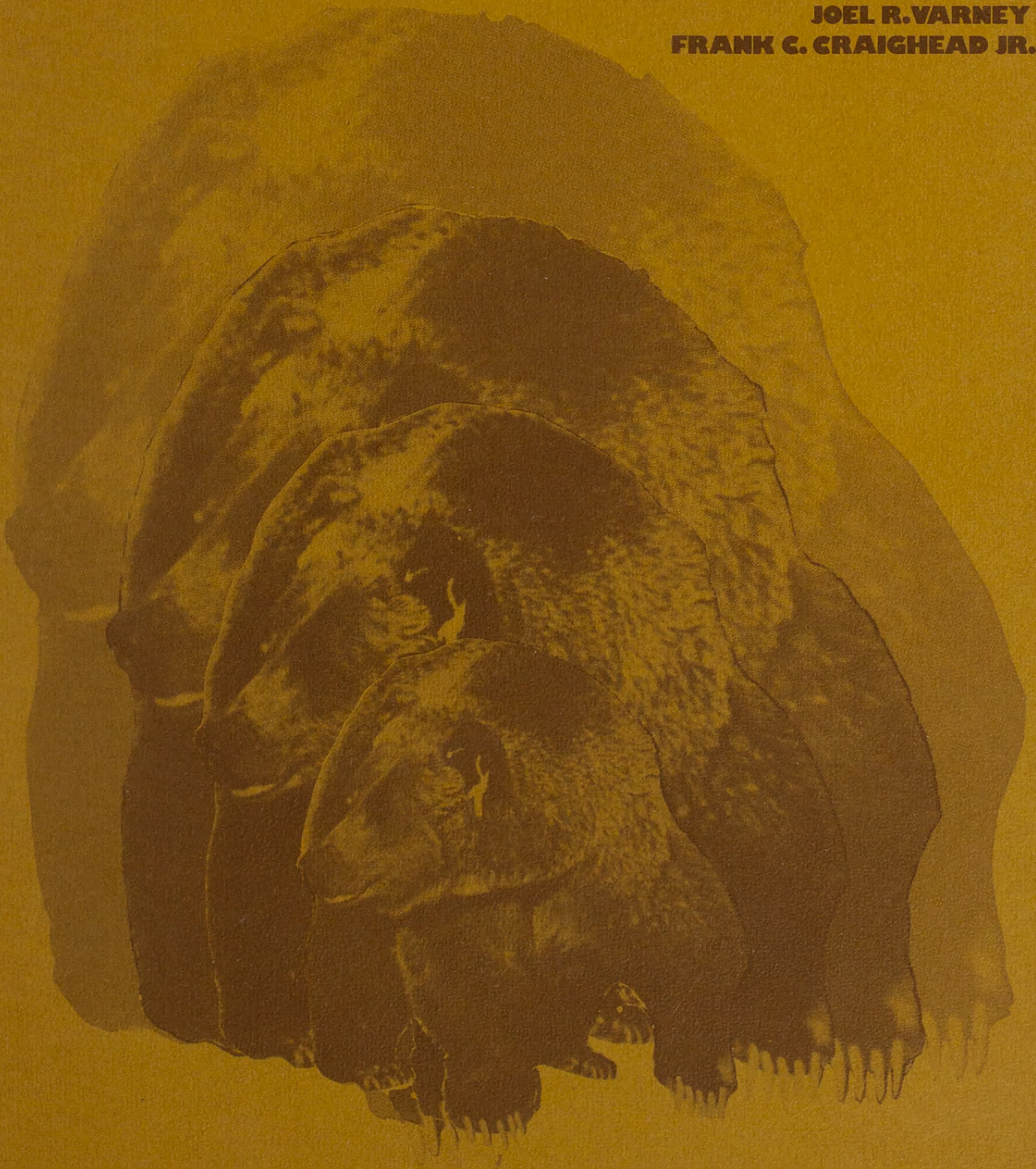

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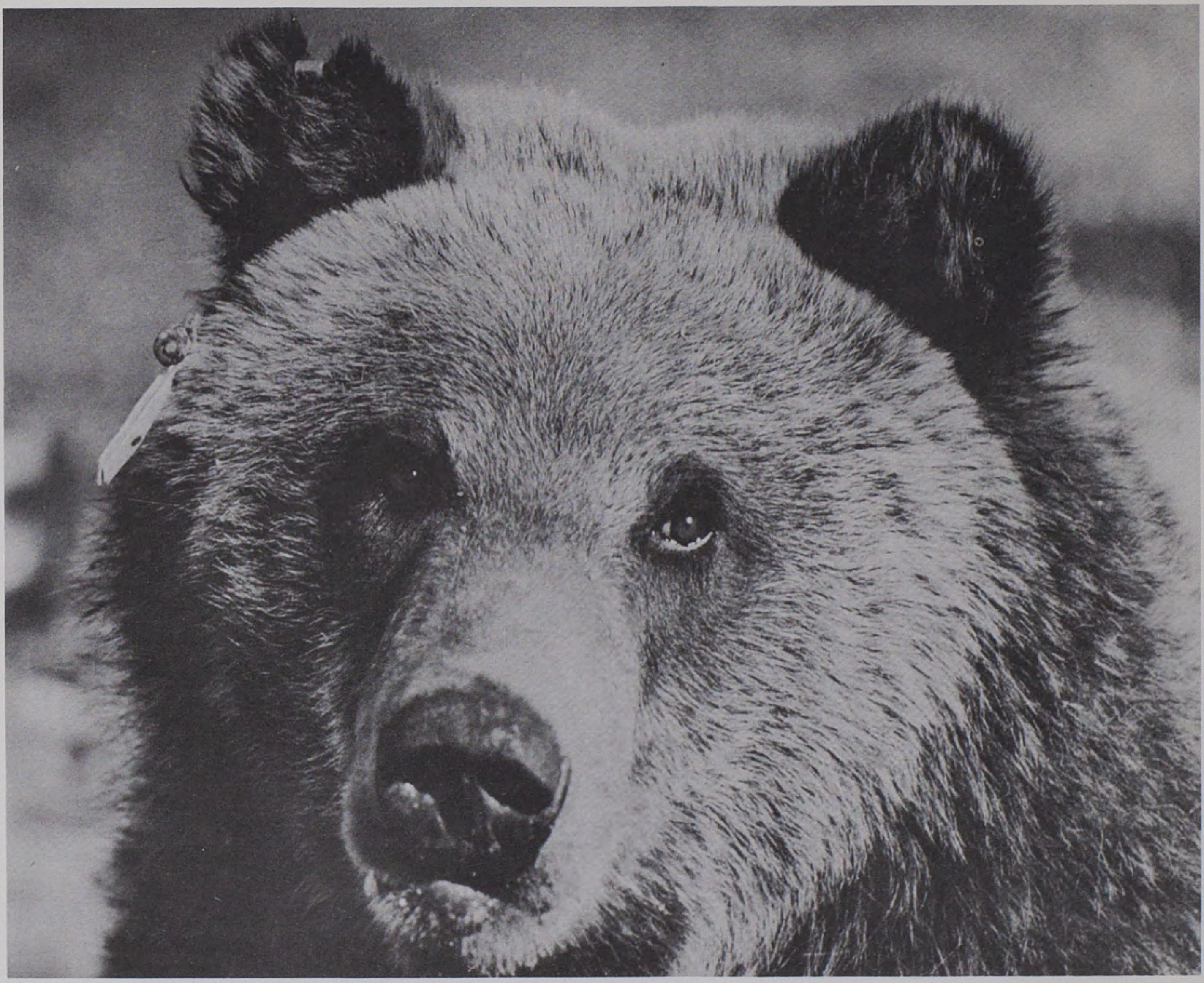


Frontispiece—Color-marked adult female grizzly

Donald ("Bud") Ozmun
Charles Pihl
and
Charles Bell
defrayed the cost of
publication

Cover design by Tom Bryan

Photographs by the authors

PREFACE

This publication is a brief description of the dynamics of a grizzly bear population. A full text with complete supporting data, descriptions of research methods, population models, and alternative simulations will be published as a *Wildlife Monograph*, a publication of The Wildlife Society.

We hope this will serve as a timely response to the urgent need for information on the status of the grizzly bear in the Yellowstone ecosystem. In order to expedite the application of our research findings, this manuscript and our other unpublished data were provided to a committee of the National Academy of Sciences-National Research Council which will make its own assessment of the grizzly bear population.

In 1969, following 10 years of intensive field study, we became concerned for the survival of the grizzly bear population in the Yellowstone ecosystem. We conveyed this concern to appropriate authorities in the National Park Service because we believed that scientists have a responsibility to present evidence and voice concern when a national resource appears threatened. Differences of opinion were reflected in a controversy that appeared detrimental to the bears. However, since critical evaluation and controversy are an integral part of the scientific procedure, we believe that resolution of this complex problem will prove beneficial to all concerned. Moreover, we are convinced that the time-lag between completion of long-term field investigations and publication must be shortened by verbal communications and by tentative evaluation of data if crucial research findings are to be properly appraised and expeditiously applied in a nation faced with burgeoning ecological crises.

ACKNOWLEDGMENTS

Research described in this report was conducted in Yellowstone National Park under a cooperative agreement between the National Park Service and the Montana Cooperative Wildlife Research Unit. The study was supported by Research Grant GB-2672 from the National Science Foundation, continuing grants from the National Geographic Society, and supporting funds, contracts and grants from the U.S. Fish and Wildlife Service, the University of Montana, the Montana Fish and Game Department, Wildlife Management Institute, National Park Service, Boone and Crockett Club, New York Zoological Society, Montana University Foundation, National Aeronautics and Space Administration, American Museum of Natural History, and the Grizzly Riders. We especially appreciate the assistance of the Yellowstone Park Company, a private concession within the Park, which provided us with housing and with a laboratory and utilities.

We extend special thanks and credit to Dr. Maurice Hornocker, Mr. Jay Sumner, Dr. Robert Ruff, and Dr. Jerry McGahan who, first as students then as research associates, worked closely with us in the field and in the laboratory. With their help, it was possible to maintain the continuity of research effort so essential for a long-term population study. The senior author is particularly indebted to Jay Sumner, whose loyalty and hard work enabled us to continue the study during 1971, 1972 and 1973 under extremely adverse conditions. Dr. Bart O'Gara cheerfully accepted extra duties at the Montana Cooperative Wildlife Research Unit to provide the senior author with time to write. We also wish to thank Harry Reynolds, Jr., Harry Reynolds III, James Claar, and Lance, Derek, Charles and Karen Craighead for their help.

The support and encouragement of many other persons made this investigation possible. Thanks are extended to Mr. Horace Albright, an outstanding Park Service Director; Mr. Lemuel Garrison, and other personnel of Yellowstone National Park; Dr. Melvin M. Payne, President of the National Geographic Society; Dr. Vincent J. Schaefer, Director, Atmospheric Science Research Center, State University of New York at Albany; Dr. Laurence M. Gould, past president AAAS; and Dr. George Jacobs, NASA. Personnel of the Montana, Idaho, and Wyoming Fish and Game Departments helped to locate and verify known grizzly bear kills.

Mr. Frank Goodyear, Mr. Donald Ozmun, and Mr. Charles Pihl made annual personal donations to our research effort that were invaluable in helping us to maintain continuity in seeking solutions to a complex resource problem.

For professional help and advice in statistical problems, population modeling and programming, we are grateful to Dr. Mark Behan, Dr. Frank Munshower, Dr. William Pierce, Dr. Don Loftsgaarden, Dr. Dave Firmage and Mr. John Mitchell.

Last but not least, we are grateful for rich memories of grizzly bears, of research and wilderness adventures, and for the comradeship that develops during a worthwhile common effort.

a population analysis of the yellowstone grizzly bears

SUMMARY

Grizzly bear population data gathered over a 15-year period in the Yellowstone Park ecosystem are summarized, and the derivation of a mathematical model of this population is described. The validity of the model is verified by comparing its behavior with that of the actual population during the period for which field data were available. The model is then used to estimate the present grizzly population and to predict future rates of growth or decline.

The results of the analysis indicate that population levels in the Yellowstone ecosystem declined rapidly during the last 4 years, and that continued mortality at the level occurring during 1970-73 will result in further decline. The best estimate demonstrates a 44.5% decline in the Yellowstone ecosystem population by 1974, from a peak of 245 grizzlies in 1967. Simulations of the dynamics of the grizzly bear population suggest that extirpation can occur rapidly when mortality rates exceed reproductive rates.

Because of the relatively small size of the Yellowstone population, its low reproductive rate, and the difficulty of annually enumerating its size, a general decline can become critical unless it is recognized and corrective action taken.

INTRODUCTION

The number of grizzly bears (*Ursus arctos horribilis*) in the United States, excluding Alaska, has rapidly declined since the early 1800's (Craighead and Craighead 1973). Before the coming of the white man, grizzly bears ranged from the Pacific Ocean to the Mississippi River and from Mexico to the Arctic Circle.

Since Lewis and Clark first saw grizzly bears on our western prairies in 1805, their numbers have steadily declined. They have disappeared from Texas, Kansas, Arizona, New Mexico, Oregon, Utah, the Dakotas and probably Colorado and Washington. In California, where there were once an estimated 10,000 grizzlies, all had vanished by 1924 (Storer and Tevis 1955). There is considerable evidence that grizzly bears may no longer exist as a viable population in the 1,643,000-acre Selway-Bitterroot Wilderness ecosystem of Idaho and Montana where they were once fairly abundant during the 1900's[1] (Wright 1907). The population history of the grizzly in California and generally throughout its range in the 48 states has been characterized by gradual reductions in numbers, followed by precipitous declines (Storer and Tevis 1955). The number now inhabiting the contiguous 48 states probably does not exceed 600 or 700. These are found only in the high mountain country and the wilderness areas of our large national parks and forests. In Alaska and western Canada, grizzly bears are still relatively abundant. But wherever grizzlies share the same habitat with humans, conflict develops (Craighead and Craighead 1971, Herrero 1971). This has placed the grizzly in a precarious position, especially within National Parks where visitor use has steadily increased.

Knowledge of the population dynamics of the species has become essential to the preservation and management of the small and relatively isolated populations inhabiting Idaho, Montana and Wyoming. This paper briefly describes the biological parameters measured in a 15-year study of a grizzly bear population, the methods of analyzing the data, and the conclusions reached.

[1]Craighead, J. J. Review of grizzly bear numbers in the Selway-Bitterroot ecosystem. Manuscript in preparation for publication.

GENERAL PROCEDURE

The vital statistics needed to develop a model and to analyze the dynamic processes occurring in a grizzly bear population were obtained in Yellowstone National Park and vicinity each year from 1959 through 1970. Employment of standardized procedures for gathering comparative data year after year insured a greater accuracy of the basic biological parameters than could have been provided by annual statistics or short-term averages. These long-term data permitted construction of a model that predicts actual population changes as closely as field data-gathering methods will allow.

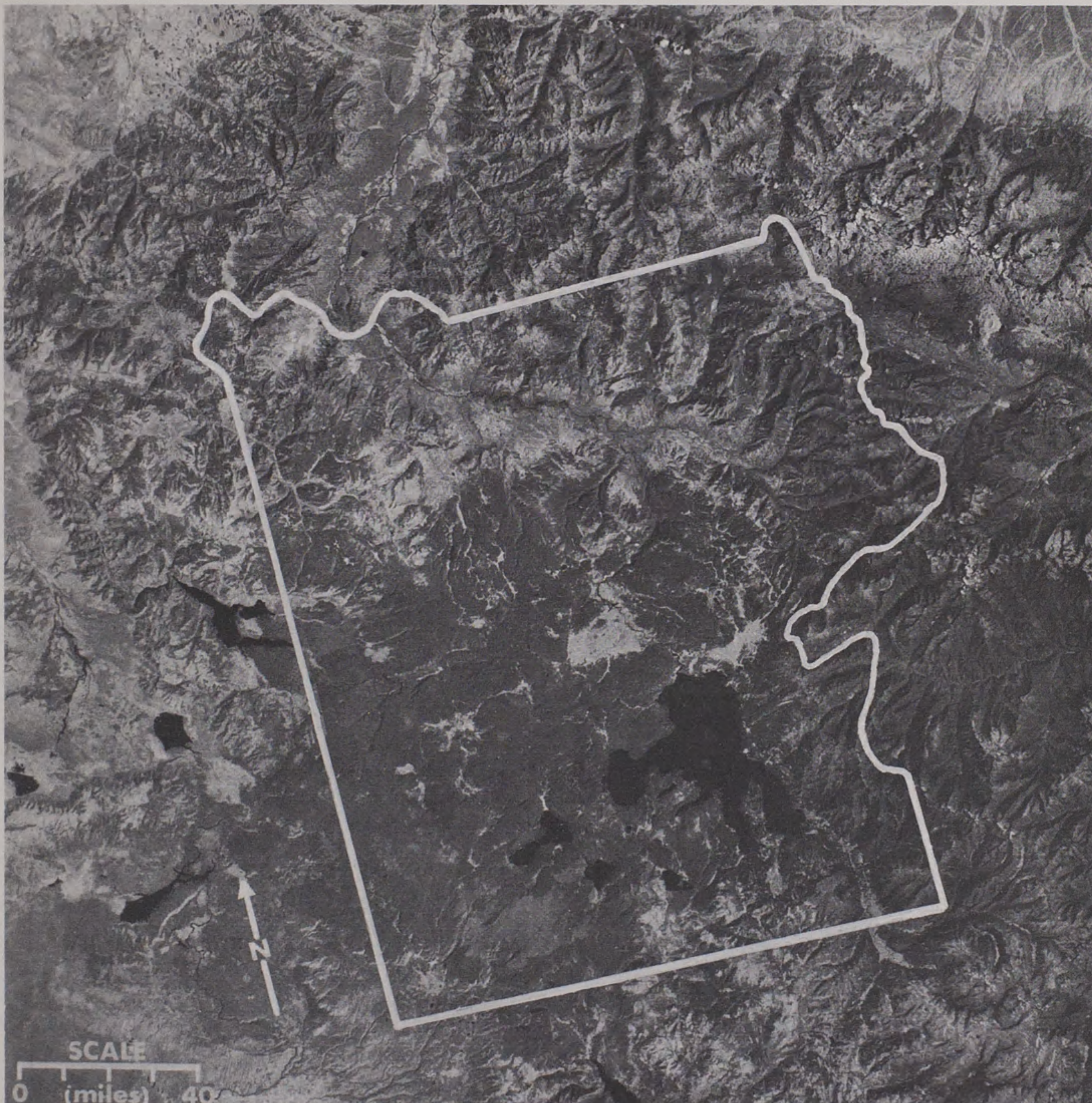


Photo courtesy of NASA

Plate 1.—Photograph of the Yellowstone ecosystem taken from 500-mile altitude by the ERTS-1 satellite. The boundaries of Yellowstone National Park are outlined. Most of the prime grizzly bear habitat lies within the park.

POPULATION STATISTICS

Approximately 41 3.5-hour censuses were made each year from 1959 through 1970 at five localities throughout the Park. Censuses were made from 1 June to 30 August, and therefore the population figures represent mid-year levels. During a 12-year period, 264 grizzly bears were captured, individually color-marked as described by Craighead *et al.* (1960), and returned to the population. Population size, age structure, and sex ratio data resulted from direct counts of bears individually recognized (Hornocker 1962, Craighead and Craighead 1967). Census counts ranged from 154 animals in 1959 to 179 in 1970 with a peak of 202 in 1966 (Table 1).

The Yellowstone grizzly bear ecosystem was calculated to be approximately 5 million acres based on the distribution of bear mortalities and sight records, and on habitat and land-use inventories. This included Yellowstone National Park, portions of Grand Teton National Park and parts of five national forests (Fig. 1 and Plate 1).

Movements of marked grizzlies, back-country

Table 1—Age structure of the grizzly population throughout Yellowstone National Park, 1959-1970

	1959		*1960*		*1961*		*1962*		*1963*		*1964*		*1965*	
Age Class	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*
Cubs	26	16.9	35	20.8	30	18.1	39	25.2	40	22.1	24	13.0	40	21.4
Yearlings	23	14.9	15	8.9	17	10.2	13	8.4	29	16.5	30	16.2	20	10.7
2-yr. olds	17	11.0	5	2.9	17	10.2	9	5.8	11	6.3	30	16.2	34	18.2
Sub-adults (3-4 yrs.)	—	—	12	7.1	23	13.9	35	22.6	25	14.2	19	10.3	23	12.3
Adults	88	57.2	102	60.3	79	47.6	59	38.0	72	40.9	82	44.3	70	37.4
TOTALS	154	100.0	169	100.0	166	100.0	155	100.0	177	100.0	185	100.0	187	100.0

	1966		*1967*		*1968*		*1969*		*1970*		*Ave. No. & % 1959-67 (9-yr. period)*		*Ave. No. & % 1968-70 (3-yr. period)*	
Age Class	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No. of Indiv.*	*% of Total*	*No.*	*%*	*No.*	*%*
Cubs	32	15.8	30	17.1	32	17.7	28	14.4	21	11.7	32.9	18.6	27.0	14.6
Yearlings	36	17.8	24	13.7	19	10.5	27	13.8	18	10.1	23.0	13.0	21.3	11.5
2-yr. olds	17	8.4	23	13.1	15	8.3	18	9.2	15	8.4	18.1	10.2	16.0	8.6
Sub-adults (3-4 yrs.)	45	22.3	26	14.9	25	13.8	24	12.3	31	17.3	26.0	14.7	26.7	14.4
Adults	72	35.7	72	41.1	90	49.7	98	50.3	94	52.5	77.3*	43.7	94.0	50.8
TOTALS	202	100.0	175	100.0	181	100.0	195	100.0	179	100.0	177	100.0	185	99.9

*8-year average since adults and sub-adults were not distinguished in 1959.

censuses, and mortality records showing the distribution of marked to unmarked animals indicated that the individuals being censused represented a large proportion of the entire population of grizzly bears inhabiting the 5-million-acre ecosystem. Calculations based on the relationship of the marked and unmarked kill of grizzlies inside and outside the Park confirmed that we were censusing approximately 77% of the entire ecosystem population.

Age Structure

The ages of individual animals were recorded during each of 367 3.5-hour censuses made from 1959 through 1967. Many marked animals were of known or established age and could be recognized year after year by individualized color markers (Plates 2 and 3). The age of some unmarked animals could be determined because they were members of marked litters or because they developed diagnostic natural markings or scars that made them identifiable at close range (Plate 4). Most observations were made at distances under 200 feet. Changes in age structure from year to year are shown in Table 1. The average age composition was 18.6% cubs, 13.0% yearlings, 10.2% 2-year olds, 14.7% 3- and 4-year olds, and 43.7% adults. This age structure was used to develop Fig. 2. A further breakdown of the adult age structure was obtained by randomly capturing and aging 52 adults (27 males and 25 females). Fourth premolars extracted from each captured adult before release[2] were sectioned and cementum layers counted to determine age (Scheffer 1950, Craighead *et al.* 1970). The sample of 52 aged adults was increased to 60 (32 males and 28 females) by including eight animals captured and aged as sub-adults that were known to be adult members of the population in 1966. This adult age structure and the age structure from 0.5 to 5.5 years were then combined and applied to an average population level of 177 animals (Fig. 2) in order to construct an age- and sex-specific life table.

[2]Craighead, J. J. Aging a grizzly bear population. (Manuscript in preparation for publication.)

Sex Ratios

From 1959 through 1970 sub-adult grizzlies were sexed following capture and classified by sex as cubs, yearlings, 2-, 3-, and 4-year olds (Table 2). The percentages of males to females in these sub-adult classes were used in the population breakdowns. Males predominated over females in all sub-adult age classes.

Sex ratios for adults were determined from observations of marked and unmarked animals. Unmarked adults, unlike sub-adults, can be sexed in the field at close range by size and conformation and by observing their reproductive behavior (Plate 5). Among 577 observations of adult grizzlies, most of them recognized as individuals, 53.7% were females and 46.3%

Table 2—Sex-age designation of marked sub-adult grizzlies, 1959-1971

	Number of Individuals			*Percent*	
Age Class	*Males*	*Females*	*Totals*	*Males*	*Females*
Cubs	46	32	78	59	41
Yearlings	38	22	60	63	37
Two-year olds	21	17	38	55	45
Three-year olds	20	13	33	61	39
Four-year olds	6	4	10	60	40

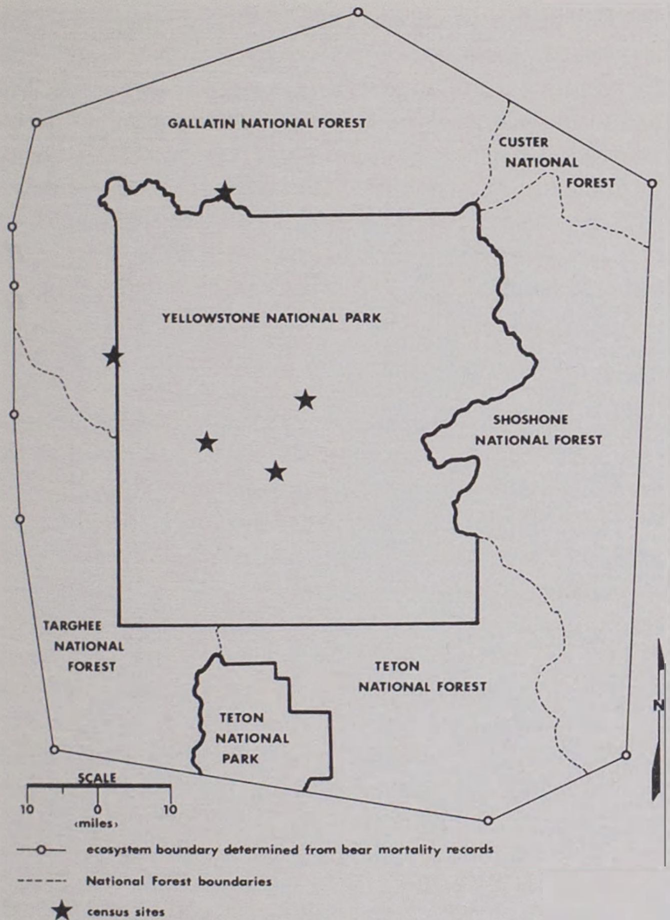


Figure 1.—Yellowstone grizzly bear ecosystem.

were males (Table 3). This adult sex ratio obtained over a 7-year period is considered representative of the population and was used to convert age structure to age-sex structure (as in Table 9).

Sex ratio of cubs was recorded by capturing and sexing them at 5 to 8 months of age. Among 78 cubs captured and sexed during a 12-year period, 59% were males and 41% females (Table 4). A comparison of the data in Tables 2 and 3 shows that a differential sex mortality is operative among adults. This may be due to selective hunting of males and to higher mortality caused by greater movement. This is substantiated by a record of 137 adult mortalities, of which 54.7% were males. The fact that the adult female segment of the population increases in relation to the adult male segment has important effects on the potential growth of the population. The cumulative cub sex ratio of 0.59 males to 0.41 females may result from differential mortality of females or from sampling procedure.

Reproductive Rates

A reproductive rate is the number of cubs produced per adult female per year calculated by dividing litter size by length of reproductive cycle. An average reproductive cycle for females in the Yellowstone population was derived from reproductive histories of 30 marked animals. Among these, all but five were aged by the cementum layer technique (Craighead *et al.* 1970). Number of litters, total number of cubs per litter, number and length of reproductive cycles and length of the reproductive period in years were recorded for each of the 30 females (Table 5). Fig. 3 shows, for each female, the observation period, pregnancies, and the female's age at the time observations were made. The reproductive period for each female is the sum of its reproductive cycles. The number of cycles per female varied from one to four and totaled 68 for all 30 animals during a cumulative reproductive period of 218 years.

To this period must be added 13 years representing the pre-pregnancy period of seven females known to be older than 4.5 years at their first pregnancies. The pre-pregnancy period represents the period between the earliest known pregnancy (age class 4.5) and the actual age at which the first pregnancy occurred in specific females (Craighead *et al.* 1969). The average reproductive cycle of the 30 female grizzlies was 3.40 years [(218 + 13 years)/68 cycles]. The reproductive cycle of individual females varied in length from 2 to 7 years and the pre-pregnancy period varied from 1 to 4 years. Reproductive rates for the 30 females ranged from a low of 0.286 to a high of 1.500. An average reproductive rate for the 30 females was 0.658 (Table 6).

Average annual litter sizes were determined by including observations from an additional 25 marked females with the 30 shown in Table 5 to obtain a larger sample size. Some breaks in observational continuity present in the group of 25 made the data unsuitable for calculating reproductive cycles, but usable for compiling values for annual litter sizes. Table 7 shows the number of females with litters, the total cubs with the females, and the average litter size that prevailed each year from 1959 through 1973. The average annual litter size varied from 1.75 in 1970 to 2.50 in 1963 and 1967.

Dividing the average annual litter sizes by the average reproductive cycle (3.40 years) gives the reproductive rates shown for each year in Table 8. The average reproductive rate of 0.626 for all females is lower than that obtained for the 30 females recorded in Table 5 and calculated in Table 6. Because of the increased litter sample, we considered this rate and the annual reproductive rates to be the more accurate of the two.

Unfortunately, we do not have quantitative data on the

Table 3—Sex ratios determined from observation of marked and unmarked adult grizzlies, 1964-1970 (adult sex ratio for population = .54F to .46M)

Year	Number of Males	Number of Females	Total	Sex Ratios Males	to Females	Percent Males	to Females
1964	34	48	82	71	100	41.5	58.5
1965	27	43	70	63	100	38.6	61.4
1966	29	43	72	67	100	40.3	59.7
1967	31	40	71	78	100	43.7	56.3
1968	44	46	90	96	100	48.9	51.1
1969	53	45	98	118	100	54.1	45.9
1970	49	45	94	109	100	52.1	47.9
1964-1970	267	310	577	86 to	100	46.3 to	53.7

number of females with litters for 1971, 1972, and 1973 comparable with those from the first 12 years of the study. We can calculate reproductive rates from Cole's data (Cole 1973a, b), but must recognize that the data for 1971 and 1972 are probably optimistic because individual bears and litters were not identified.

Consolidating the data into 3-year periods (Table 7) revealed little variation in the number of females with litters from 1959 through 1967, but a considerable drop in numbers from 1968 through 1973. There was a corresponding decline in number of cubs and thus in average litter size. A Mann-Whitney U-Test comparing the number of cubs with females per year from 1959-69 with those from 1970-73 indicates a significant difference between the two groups ($\alpha \geqq 0.05$ and $z = 2.162$). There was also a significant difference between average annual litter sizes ($\alpha \geqq 0.05$ and $z = 2.550$). We attribute this decline in productivity (especially from 1970 through 1973), which is reflected in the number of pregnant females and the average litter size, to the stresses placed on the population by the abrupt closing of the open pit garbage dumps (Craighead and Craighead 1971).

Other statistical tests were made to determine if any biases were affecting the reproductive rate calculations summarized above. Spearman Rank Correlation Coefficients (SRCC) were calculated relating ages of females to the number of cubs in their litters, and to the length of their reproductive cycles. No significant correlations were found. SRCC's were also calculated to test whether immobilizing drugs had any effect on long-term productivity of females. These, too, were statistically insignificant. We conclude that no significant biases were introduced into the calculations of litter size, length of reproductive cycle, or reproductive rate by the ages of the females sampled or by the use of immobilizing drugs.

Mortality and Survivorship Rates

Mortality was measured in two ways: first by changes in sex-age structure from year to year, and second by verifying and recording actual deaths. Mortality and survivorship rates for the population were obtained by using age structures, sex ratios and census data described earlier to construct an age- and sex-specific life table for the period 1959-67 (Table 9). Data for this 9-year period were used, rather than data for a longer period of time, because new management procedures greatly increased the annual death rate of the population after the summer of 1967. The survivorship rates for the 1959-67 period characterized a population in stable age distribution. The age structure data in Table 1 and Fig. 2 were converted to an age- and sex-specific structure by applying the sex

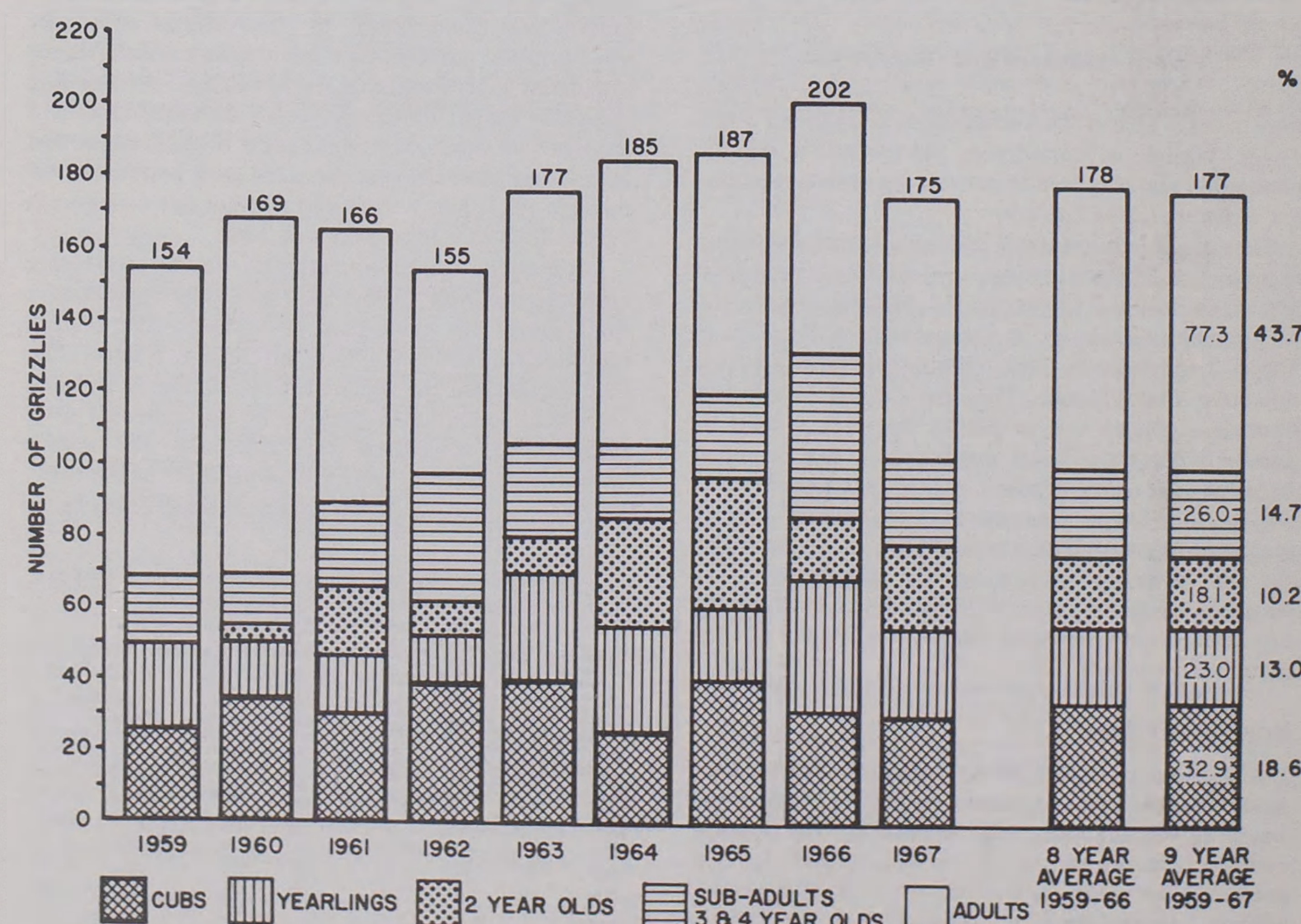


Figure 2.—Age structure of the Yellowstone grizzly bear population, 1959-67.

Plate 2.—Cub with numbered ear tag and color-marker of polyethylene braided rope and polyvinyl tape. Variations in rope and flag colors and placement of numbered ear tags permitted the use of numerous individualized combinations.

ratios from Tables 2, 3 and 4 and then smoothing this to the form shown in Table 9. Mortality and survival are expressed through the sex-age structure of the population and were converted to the number annually dying and the number annually surviving in a population of 178 animals. The sub-adult age classes (0.5 to 4.5) shown in column 2 of Table 9 represent 9-year averages for the population (Table 1); the adult age classes (5.5 to 25.5) represent one-time samples of 60 adults as described earlier.

The age-specific mortality shown in Table 9 represents death from all causes. Among these deaths, some were known and recorded; others were unknown and unrecorded except as they were reflected in the age structure.

Each year from 1959 through 1973, all known grizzly bear deaths were recorded (Table 10). Because it was difficult to obtain the precise ages of these animals, they have been grouped into three classes: sub-adults, adults, and a class of unknown sex and age. In general, the adult and sub-adult classes represent the reproductive and non-reproductive periods in the life of a female grizzly bear. From 1959 through 1967, a total of 170 known deaths averaged 18.9 bears per year or a 10.6% known mortality in a population of 178 animals. A total of 189 known deaths occurring from 1968 through 1973 averaged 31.5 bears per year with maximum deaths of 53 and 48 grizzlies in 1970 and 1971, respectively. Known deaths for the 15-year period (1959-73) totaled 359. Deaths of adult and sub-adult females alone increased from 39.8% (51/128) during 1959-67 to 44.7% (71/159) for the 1968-73 period.

The mortality percentages by sex and age among the 359 known deaths show the adult and sub-adult deaths to be equal (Table 11). Forty-six percent of all deaths were males, 34% were females and 20% were of unknown sex. In all probability, the differential sex mortality has led to the unbalanced adult sex ratio of 47% males to 54% females (Table 3). The preponderance of males to females in the sub-adult age structure (Table 2) does not reflect the differential male mortality among sub-adults. This may be due to sampling error.

In summary, Table 9 provides an average yearly total of all deaths for both sexes and each age class. This includes recorded deaths averaging 18.9 per year, as well as deaths derived from the age structure averaging 14.3 per year. Table 10 provides a record of the annual recorded deaths by sex and age, while Table 11 shows the percent of known mortality in those categories. The survivorship calculations (with modification of these to accommodate recorded mortalities when they deviated from average

Table 4—Progressive summary of sex ratios from captured cubs, 1959-1970 (cub sex ratio for population = .59M to .41F)

Year	Number Sexed		Cumulative Number Sexed		Cumulative Sex Ratios of Cubs Sexed		Cumulative Percentages of Cubs Sexed	
	Males	Females	Males	Females	Males	Females	Males	Females
1959	2	2	2	2	100	100	50	50
1960	4	2	6	4	150	100	60	40
1961	6	7	12	11	109	100	52	48
1962	7	2	19	13	146	100	59	41
1963	6	1	25	14	179	100	64	36
1964	4	2	29	16	181	100	64	36
1965	1	0	30	16	187	100	65	35
1966	1	1	31	17	182	100	65	35
1967	5	6	36	23	156	100	61	39
1968	7	6	43	29	148	100	60	40
1969	0	0	43	29	148	100	60	40
1970	3	3	46	32	144	100	59	41

rates) and calculations of yearly increments based on reproductive rates provide the basis for describing the way grizzly bears enter and leave age classes from year to year.

Longevity

Information on longevity was obtained by aging adults using the cementum layer technique (Craighead *et al.* 1970). The oldest live bear captured and aged was 25.5; this age represents longevity for the population. The maximum reproductive age established for a female was 22.5; at this age, she produced two cubs. She was observed at age 24.5 without offspring.

POPULATION MODEL CONSTRUCTION

The age- and sex-specific survivorship rates summarized in Table 9 provide the basic data for a mathematical model of the grizzly bear population. Beginning with an initial population, the number of animals in each age and sex class which will survive from one year to the next are given by the survivorship probabilities (Px). The number of cubs born each year can be predicted by counting the number of adult females in the population each year and applying the proper reproductive rate and sex ratio.

These data were incorporated into a digital computer program which calculated the changes occurring in the population on a year-by-year basis, to form a deterministic mathematical model. The model was then used to study the behavior of the population, to determine the effects of changes in various biological parameters, and to predict the overall population trend after 1970 when field census data were no longer being taken.

In addition to the basic biological parameters, data measuring the effects of external pressure on the population from hunting and control actions were incorporated into the model. During the 1959-67 base period from which the survivorship rates were derived, recorded mortality accounted for slightly more than half of the total yearly deaths occurring in the population. Recorded mortalities averaged 10.6% of the censused population each year. To accurately simulate the effect of having substantially more or fewer recorded mortalities than the average predicted by the survivorship rates, adjustments were made in years when recorded mortalities deviated from the average.

Plate 3.—Adult female with color-marker. Most identifications were made at distances less than 200 feet; however, under ideal conditions, color combinations could be read at one-fourth to one-third of a mile with a 20X scope.

Adjustments to Biological Parameters

Minor adjustments in cub sex ratios and survivorship rates were made before incorporating these biological parameters into the model. This made the model's behavior simulate more closely that of the actual population.

The cub sex ratio used for the model was 50:50 (male to female) rather than the 59:41 observed value shown in

Table 5—Reproductive rates of 30 marked female grizzlies calculated from 68 reproductive cycles, 1959-1972 (Note: Reproductive cycles are calculated from pregnancy to assumed pregnancy)

Bear No.	*Age* Marked*	*Number of Reproductive Cycles*						*Total Cycles*	*Reproductive Period in Years*	*No. Cubs*	*Reproductive Rates*
		2-Yr	*3-Yr.*	*4-Yr*	*5-Yr*	*6-Yr*	*7-Yr*				
5	1.5	—	1	1	—	—	—	2	7	5	0.714
7	12.5	—	2	1	—	—	—	3	10	8	0.800
10	2.5	—	1	1	—	—	—	2	7	4	0.571
15	1.5	—	3	—	—	—	—	3	9	5	0.556
34	14.5	1	1	—	1	—	—	3	10	6	0.600
39	5.5	—	1	1	1	—	—	3	12	7	0.583
40	1.5	2	1	—	—	—	—	3	7	7	1.000
42	5.5	2	2	—	—	—	—	4	10	8	0.800
65	Adult	3	—	—	—	—	—	3	6	9	1.500
84	Adult	1	—	1	—	—	—	2	6	5	0.833
96	3.5	—	3	—	—	—	—	3	9	8	0.889
101	4.5	2	—	1	—	—	—	3	8	4	0.500
112	8.5	—	1	—	—	1	—	2	9	5	0.556
120	12.5	—	—	1	—	—	1	2	11	4	0.364
125	5.5	—	4	—	—	—	—	4	12	10	0.833
128	10.5	2	2	—	—	—	—	4	10	13	1.300
144	0.5	1	—	1	—	—	—	2	6	4	0.667
150	4.5	—	—	1	1	—	—	2	9	5	0.556
163	1.5	1	—	—	—	—	—	1	2	2	1.000
172	11.5	1	2	—	—	—	—	3	8	7	0.875
173	2.5	1	1	—	—	—	—	2	5	3	0.600
175	10.5	1	2	—	—	—	—	3	8	4	0.500
175B	Adult	—	2	—	—	—	—	2	6	4	0.667
200	3.5	—	—	1	—	—	—	1	4	2	0.500
44	Adult	—	—	—	—	—	1	1	7	2	0.286
140	8.5	—	—	—	1	—	—	1	5	3	0.600
141	1.5	—	1	—	—	—	—	1	3	2	0.667
160	Adult	—	—	—	—	1	—	1	6	2	0.333
180	11.5	—	1	—	—	—	—	1	3	3	1.000
187	1.5	—	1	—	—	—	—	1	3	1	0.333
Totals	—	18	32	10	4	2	2	68	218	152	

*In years; bears designated as "Adult" were assumed to be at least 4.5 years of age.

Table 4. We were unable to account for so large a sex imbalance on theoretical grounds and did not observe any factors which would have favored survival of male cubs during the first 4 months of life. Reproductive studies of *Ursus arctos* in zoos (Dittrich and Kronberger 1963) tend to support an even sex ratio. Consequently, we attributed our observed imbalance to sampling procedures and used the 50:50 ratio in the model.

Trial runs were then made with the model for the 1959-67 base period in order to check its population predictions against census data for the same period. The growth rate of the actual population was estimated by fitting a geometric growth curve to the census data with the least-square method (Caughley 1967). The results are shown in Fig. 4, and indicate that the population was increasing at an average rate of 2.4% per year during this period.

The intrinsic growth rate properties of the model were then investigated. This was done by solving an expression relating female age-specific survivorship rates and reproductive rates for a population in stable age distribution (Mertz 1970). The growth rate of the model was slightly low. After careful consideration, the survivorship probabilities for cubs used in the model were increased to 0.8, to compensate for dispersal of some yearlings weaned in May before the annual censuses were begun. These yearlings, if not recorded in the age structure, would have lowered the first-year survivorship values.

The simulated intrinsic growth rate with this change is shown as a function of reproductive rate (Fig. 5). The average observed reproductive rate as calculated from Table 8 for the 1959-67 period was 0.651. Fig. 5 shows that with this reproductive rate the model predicts a 2.3% growth rate, which is very close to the 2.4% actual rate inferred from the census data.

In addition to growth rate, other behavioral characteristics of the model were compared with the census data to determine if they simulated the actual population characteristics in all measurable aspects. These included checks of long-term age distribution changes and a comparison of random yearly population fluctuations, predicted by a stochastic version of the model, with actual yearly variations in population size. In all cases we found good agreement between the predictions of the model and the actual behavioral characteristics of the population we had observed and recorded. We concluded that the model accurately simulates the behavior of the grizzly bear population.

A summary of the parameters used in the final population model is presented in Table 12. The cub sex ratio (Item 3) and the cub survivorship rate (Item 7, line 1) were the only modifications to the observed biological parameters. Items 1 and 2 of Table 12, which are the bases for selecting the size and age-sex structure of the starting population, will be discussed in the following section. Item 5 of Table 12 is a rearrangement of the recorded mortalities shown in Table 10 into male sub-adult (MSA), male adult (MA), and female sub-adult (FSA) and female adult (FA) categories. Deaths of bears of unknown age or sex were allocated proportionately into the appropriate categories on the basis of the knowns in each. Item 6 of Table 12 presents the ratios of recorded mortalities to the population average for the 1959-67 period. These were used to calculate the expected number of known mortalities in each age-sex category for yearly adjustment when recorded mortalities were higher or lower than the average for the base period.

Selection of Starting Population for Simulations

We used the year 1959 as a starting point for simulation runs using the population model. This enabled us to compare the predicted population levels with the census data for the years 1959 through 1970 and thus check on the model's behavior. An alternative, to begin in 1970 and project to 1974, required that more assumptions be made for age and sex distribution of the starting population than were otherwise necessary.

The relative age and sex distribution of the 1959 starting population is proportional to the figures given in Table 9. These are averages for the 1959-67 base period and were considered to be more representative of the true distribution than actual census figures, since the latter could have random sampling errors in any one year. In addition, the field data from any one year were not sufficient to determine the complete age and sex

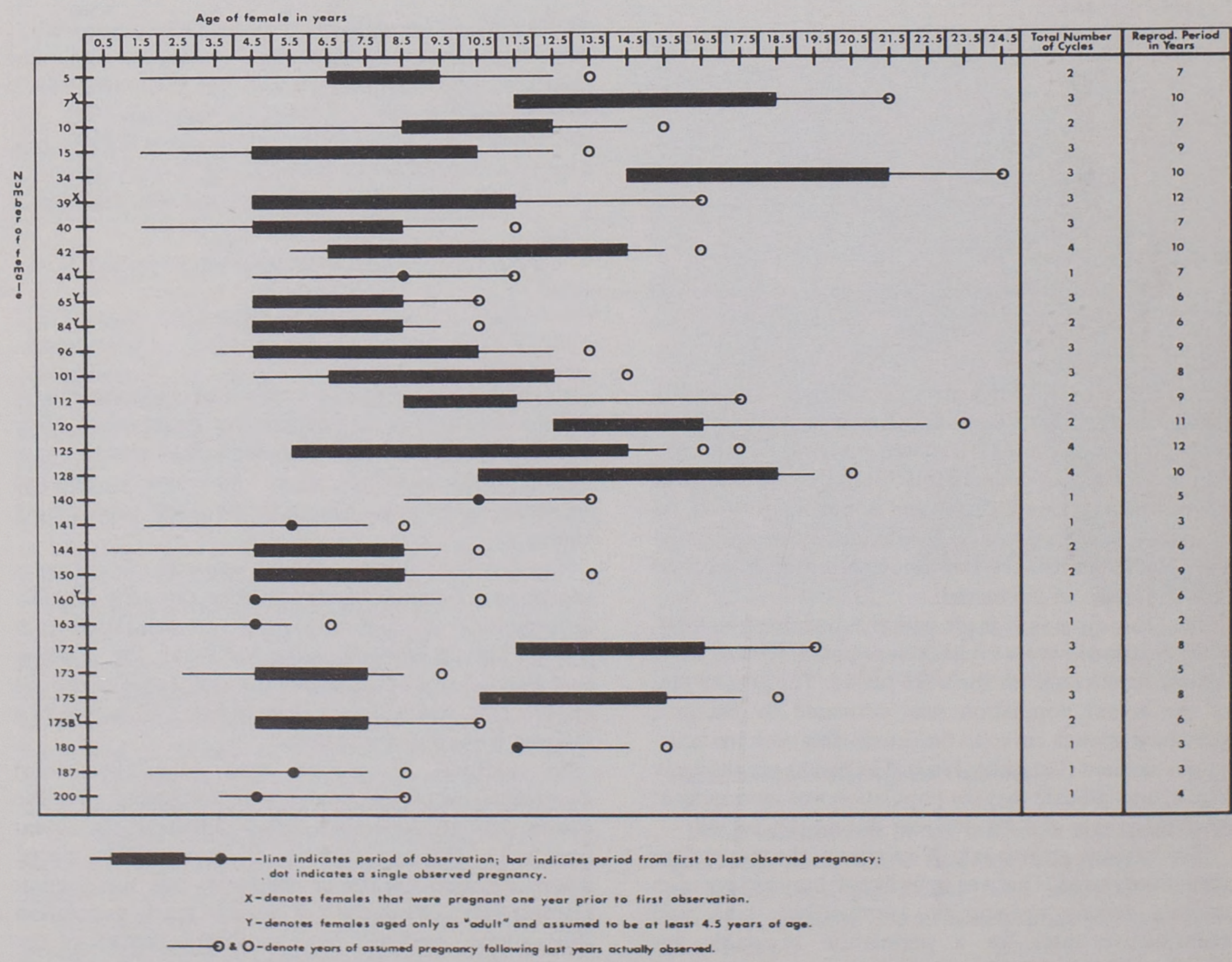


Figure 3.—Relation of recorded reproductive cycles and reproductive periods to ages of 30 female bears.

distribution for a starting population. The age and sex distribution in Table 9 was derived from data spanning portions of the entire period of the study, as explained earlier.

We considered several alternatives for determining the total size of the 1959 starting population. One choice was to use the 1959 census figure. This was discarded because of the possibility of sampling error in any one year.

A second alternative, to use the 1959 population obtained by fitting the growth curve to census data as shown in Fig. 4, avoided sampling errors. This gave a figure of 158 animals. However, while curve-fitting provided an accurate estimate of growth rate, it could not be used to obtain absolute population figures since the smoothed curve gave a value for some years below the actual. The problem arises because only a certain proportion of the total population was counted in the censuses. If the proportion remains relatively constant from year to year, the growth rate can be calculated without knowing what the proportion is; it must be known, however, to arrive at the true population size in any given year. For example, if 90% of the population was counted in each yearly census, the most probable 1959 population would be 158/0.9 = 176 animals.

Plate 4.—Adult male showing a permanent diagnostic scar on muzzle below the right eye. Another scar below the left ear permitted identification from a profile. A number of large males were identified year after year by such natural markings.

The third alternative avoided the necessity of including the census efficiency when selecting the starting population. Simulations were run with the model, using various population sizes for 1959, until the one which resulted in the best overall fit to the 1959-67 census curve was determined. The resulting population size was 172 animals; this was the value we selected for the 1959 starting population.

PROJECTIONS WITH MODEL

Simulations of the Censused Population

A population simulation run beginning in 1959 with an initial population of 172 animals and continuing until 1974 is shown in Fig. 6. Reproductive rates recorded between 1959 and 1973 were used, and the 1974 reproductive rate was assumed to be the same as in 1973 (Table 8). Population figures are given for June of each year.

The population totals predicted by the model are compared with the yearly censuses in Fig. 7. The standard error for the fit in the 1959-67 period is 15.4 animals, or 8.8% of the average censused population during that time. The maximum difference between model predictions and census figures is 11%.

The simulation shows an increase from 172 animals in 1959 to 195 in 1967. The projected population declines after 1967. The effect of the large number of 1967 recorded mortalities (43) appears the next spring in 1968. This is followed by 2 years of slight decline, and then 2 more years of sharp population drops following the heavy mortalities in 1970 (53) and 1971 (48). The last census occurred in 1970, so we are not able to verify the projected declines in 1971 and 1972 with field data. The projected rate of decline decreases during the last 2 years, but the population trend is still downward. The model indicates that only 82 bears would be counted within the Park in June of 1974 if censuses were still being conducted under conditions similar to those during the 1960's. This represents a 58% reduction of the censused population from a peak of 195 grizzlies in 1967. We can expect no improvement unless the 1974 reproductive rate increases above the 0.544 observed in 1973 or unless other yet undetected or unresponsive compensatory processes become operative.

Population Estimates for the Yellowstone Ecosystem

The actual grizzly bear population for the Yellowstone ecosystem is higher than the minimum population figures obtained in the annual field censuses. Data on movements of color-marked and instrumented animals showed that extensive natural movements throughout the entire 5-million-acre ecosystem were common (Craighead and Craighead 1968). These data suggest that a large percentage of bears within the ecosystem moved to and from the open pit garbage dumps and were counted in the annual censuses. Moreover, the data demonstrate that the censused population did not represent a local population addicted to garbage. Our backcountry observations of grizzlies showed that during the height of seasonal concentrations of animals at the dumps (August 15 to 30) very few grizzlies were observed in the backcountry of Yellowstone and the adjoining national forest areas.

Table 6—Method of calculating an average reproductive rate for 30 adult females

Cycles							Reproductive Period (yrs)		Reproductive Rate		
2-yr	*3-yr*	*4-yr*	*5-yr*	*6-yr*	*7-yr*	*Total Cycles*	*Unmodified*	*Modified*	*No. of Cubs*	*Unmodified*	*Modified*
18	32	10	4	2	2	68	218	(+13) 231	152	0.697	0.658

Calculations

$$\frac{\text{Total Cubs}}{\text{Total No. Litters}} = \frac{152}{68} = 2.24 = \text{Ave. Litter Size}$$

$$\frac{\text{Total Reproductive Period in Years}}{\text{Total No. Cycles}} = \frac{218}{68} = 3.21 = \text{Unmodified Reproductive Cycle}$$

$$\frac{\text{Total Cubs}}{\text{Total Reproductive Period in Years}} = \frac{152}{218} = 0.697 = \text{Unmodified Reproductive Rate}$$

218 + 13 = 231 (Total Reproductive Period in Years Modified by Pre-pregnancy Data)

$$\frac{\text{Modified Total Reproductive Period in Years}}{\text{Total Number Cycles}} = \frac{231}{68} = 3.40 = \text{Average Reproductive Cycle}$$

$$\frac{\text{Total Cubs}}{\text{Modified Total Reproductive Period in Years}} = \frac{152}{231} = 0.658 = \text{Average Reproductive Rate}$$

Mullen and Booth (1969) reported similar results. However, prior to August and during autumn, we observed and radio-tracked grizzlies miles from the summer concentration areas. Movement of grizzlies to the dumps in spring and early summer, and dispersion to foraging areas and winter dens in the fall, distributed them widely throughout the ecosystem at these seasons.

Because of the difficulty of recognizing and counting individual bears, no reliable population estimates could be made from observations of bears in the backcountry. However, information on the kill of marked and unmarked animals does lend itself to analysis. From 1959 through 1970, 267 known deaths were recorded inside and outside of Yellowstone Park; 143 deaths occurred outside the Park and 124 occurred inside (Table 13). Among those dying outside the Park, 103 grizzlies were clearly marked (31) or unmarked (72) bears, while the exact designation of 40 remained undetermined.

In all, 264 grizzly bears were individually marked from 1959 through 1970. These marked grizzlies, as shown from kill statistics, represented animals from all parts of the ecosystem. Thus, the kill of marked animals outside the Park could be used to estimate a total population. The average percentages of marked and unmarked bears killed outside the Park during a 12-year period were compared with the average percentages of marked and unmarked grizzlies recorded on the censuses for the same period. The data revealed the relation of the number of marked grizzlies in the population each year to the number of those counted in the censuses each year. During a 12-year period, 39.0% of all bears censused were marked ones. We determined the relation between the percent of the marked bears counted in censuses each year to the percent of those marked animals annually killed outside the Park. From 1959 through 1970, an average of

Table 7—Computation of average litter sizes of females with cubs, Yellowstone Park, 1959-1973

Year	*Total Females with Litters*		*Total Cubs with Females*		*Ave. Annual Litter Size*	*Average Three-Year Litter Size*
1959	14		26		1.86	
1960	17	= 44	35	= 91	2.06	2.07
1961	13		30		2.31	
1962	17		39		2.29	
1963	16	= 44	40	= 103	2.50	2.34
1964	11		24		2.18	
1965	19		40		2.11	
1966	15	= 46	32	= 102	2.13	2.22
1967	12		30		2.50	
1968	13		32		2.46	
1969	14	= 39	28	= 81	2.00	2.08
1970	12		21		1.75	
Cole's Data (1973a, b)						
1971	16		31		1.94	
1972	11	= 40	22	= 77	2.00	1.93
1973	13		24		1.85	

Table 8—Calculations of reproductive rates from annual counts of females with cubs using a reproductive cycle of 3.40 years, 1959-1973 (Note: Reproductive cycle calculated from the reproductive histories of 30 marked females.)

Year	*Individual Females with Cub Litters*	*Total Cubs*	*Ave. Annual Litter Sizes*	*Annual Reproductive Rates*
1959	14	26	1.86	0.547
1960	17	35	2.06	0.606
1961	13	30	2.31	0.679
1962	17	39	2.29	0.674
1963	16	40	2.50	0.735
1964	11	24	2.18	0.641
1965	19	40	2.11	0.621
1966	15	32	2.13	0.626
1967	12	30	2.50	0.735
1968	13	32	2.46	0.724
1969	14	28	2.00	0.588
1970	12	21	1.75	0.515
1971	16	31	1.94*	0.571
1972	11	22	2.00*	0.588
1973	13	24	1.85*	0.544
Average			2.13	0.626

*Calculated from Cole's data (1973a, b)

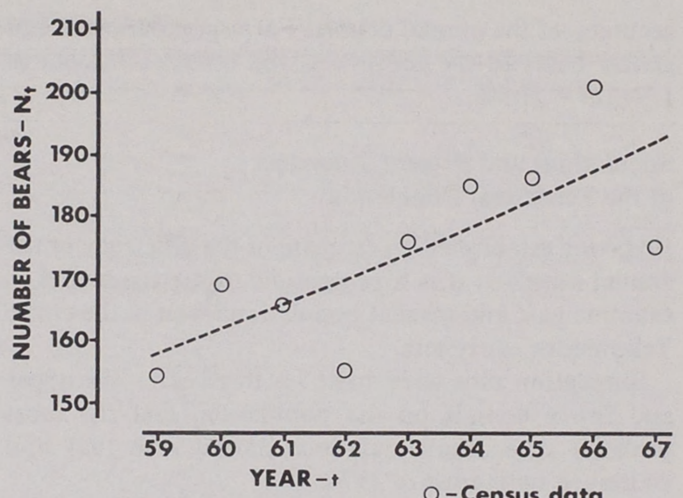
Table 9—Age- and sex-specific life table for the Yellowstone grizzly bear population, 1959-1967

MALES						
Age	*Number in Age Class*	*Number Males*	*Number Dying Age Class Dx*	*Number Surviving per Thousand Lx*	*Survivorship Rate Px*	*Mortality Rate Qx*
0.5	33.0	19.5	5.0	1000.	0.7436	0.2564
1.5	23.0	14.5	4.6	744.	0.6828	0.3172
2.5	18.0	9.9	1.4	508.	0.8586	0.1414
3.5	14.0	8.5	1.5	436.	0.8235	0.1765
4.5	12.0	7.0	3.4	359.	0.5143	0.4857
5.5	7.7	3.6	0.2	185.	0.9444	0.0556
6.5	7.4	3.4	0.2	174.	0.9412	0.0588
7.5	7.0	3.2	0.1	164.	0.9688	0.0313
8.5	6.8	3.1	0.1	159.	0.9677	0.0323
9.5	6.6	3.0	0.1	154.	0.9667	0.0333
10.5	6.3	2.9	0.1	149.	0.9655	0.0345
11.5	6.1	2.8	0.1	144.	0.9643	0.0357
12.5	5.8	2.7	0.3	138.	0.8889	0.1111
13.5	5.2	2.4	0.3	123.	0.8750	0.1250
14.5	4.5	2.1	0.5	108.	0.7619	0.2381
15.5	3.5	1.6	0.4	82.	0.7500	0.2500
16.5	2.6	1.2	0.2	62.	0.8333	0.1667
17.5	2.2	1.0	0.2	51.	0.8000	0.2000
18.5	1.7	0.8	0.2	41.	0.7500	0.2500
19.5	1.4	0.6	0.1	31.	0.8333	0.1667
20.5	1.1	0.5	0.1	26.	0.8000	0.2000
21.5	0.8	0.4	0.1	21.	0.7500	0.2500
22.5	0.6	0.3	0.1	15.	0.6667	0.3333
23.5	0.4	0.2	0.1	10.	0.5000	0.5000
24.5	0.2	0.1	0.1	5.	0.5000	0.5000
25.5	0.1	0.1	0.1	3.	0.0000	1.0000
TOTALS	178.0	95.4	19.6			

FEMALES						
Age	*Number in Age Class*	*Number Females*	*Number Dying in Age Class Dx*	*Number Surviving per Thousand Lx*	*Survivorship Rate Px*	*Mortality Rate Qx*
0.5	33.0	13.5	5.0	1000.	0.6296	0.3704
1.5	23.0	8.5	0.4	630.	0.9529	0.0471
2.5	18.0	8.1	2.6	600.	0.6790	0.3210
3.5	14.0	5.5	0.5	407.	0.9091	0.0909
4.5	12.0	5.0	0.9	370.	0.8200	0.1800
5.5	7.7	4.1	0.1	304.	0.9756	0.0244
6.5	7.4	4.0	0.2	296.	0.9500	0.0500
7.5	7.0	3.8	0.1	281.	0.9737	0.0263
8.5	6.8	3.7	0.1	274.	0.9730	0.0270
9.5	6.6	3.6	0.2	267.	0.9444	0.0556
10.5	6.3	3.4	0.1	252.	0.9706	0.0294
11.5	6.1	3.3	0.2	244.	0.9394	0.0606
12.5	5.8	3.1	0.3	230.	0.9032	0.0968
13.5	5.2	2.8	0.4	207.	0.8571	0.1429
14.5	4.5	2.4	0.5	178.	0.7917	0.2083
15.5	3.5	1.9	0.5	141.	0.7368	0.2632
16.5	2.6	1.4	0.2	104.	0.8571	0.1429
17.5	2.2	1.2	0.3	89.	0.7500	0.2500
18.5	1.7	0.9	0.1	67.	0.8889	0.1111
19.5	1.4	0.8	0.2	59.	0.7500	0.2500
20.5	1.1	0.6	0.2	44.	0.6667	0.3333
21.5	0.8	0.4	0.1	30.	0.7500	0.2500
22.5	0.6	0.3	0.1	22.	0.6667	0.3333
23.5	0.4	0.2	0.1	15.	0.5000	0.5000
24.5	0.2	0.1	0.1	7.	0.5000	0.5000
25.5	0.1	0.1	0.1	4.	0.0000	1.0000
TOTALS	178.0	82.7	13.6			

30.1% of all bears killed outside the Park were marked ones. We can hypothesize that the kill of marked bears outside the Park is random. If so, the average percent of marked bears killed over an extended period of years should equal the average percent of marked grizzlies counted in the censuses if all bears in the ecosystem moved to the census sites and were counted. A percent kill of marked grizzlies outside the Park equal to the percent of marked grizzlies counted in censuses would indicate a total census of all bears. A discrepancy would suggest that not all bears were counted; the approximate number must then be calculated.

The calculation for the total ecosystem population was made by letting X represent unmarked bears that never visited the dumps and thus were never counted in yearly censuses. The total ecosystem population is then $177 + X$.



$N_t = N_0 e^{rt} = 158.2\, e^{.024\,(t-59)}$

Correlation Coefficient = 0.752

Standard Error = 11.2

Growth Rate = $\ln^{-1}(r)$ = 1.0243 = 2.43% per year

Slope Standard Deviation (S_b) = 8.06×10^{-3}

Figure 4.—Regression curve fitted to census data.

We must determine how large X must be before the ratio of marked bears to total population is equal to the ratio of marked bears in the kill outside the Park. The average ratio of marked bears observed in yearly censuses was 39%, for a yearly average of 69 animals. The ratio of marked bears killed outside the Park was 31/103 = 0.301. The total ecosystem population is then 69/0.301 = 229 animals and X = 229-177 = 52 animals that were not counted in the annual censuses.

Since the average number of bears censused during the 1959-70 period was 177, we can now calculate the

Table 10—Annual mortality of grizzly bears in the Yellowstone ecosystem, 1959-1973

	Adults			*Sub-Adults*			*Age Unknown*			
Year	*M*	*F*	*U*	*M*	*F*	*U*	*M*	*F*	*U*	*Total*
1959	5	1	1	2	2	0	0	0	1	12
1960	3	4	2	4	2	7	1	0	1	24
1961	1	1	1	7	4	4	1	1	1	21
1962	1	4	0	4	5	1	0	0	0	15
1963	2	3	0	4	2	2	2	0	0	15
1964	3	1	0	4	1	3	0	0	0	12
1965	2	3	0	6	2	0	1	0	1	15
1966	1	0	0	5	0	2	1	0	4	13
1967	2	3	2	6	1	3	9	11	6	43
Sub total	20	20	6	42	19	22	15	12	14	170
1968	9	2	1	2	3	1	0	0	3	21
1969	8	6	0	3	3	1	1	1	0	23
1970	10	13	0	11	11	5	2	0	1	53
1971	15	11	1	4	6	1	5	0	5	48
1972	10	7	1	3	3	2	0	0	1	27
1973	3	3	0	2	2	0	0	0	7	17
Sub total	55	42	3	25	28	10	8	1	17	189
TOTAL	75	62	9	67	47	32	23	13	31	359

accuracy of the annual counts. For a population of 229 grizzly bears in the ecosystem, the census efficiency is 177/229 = 77.3%.

Simulations and Present Estimates of the Ecosystem Population

Having established an estimate of the efficiency of the annual censuses, it is now possible to use the model to examine past and present population levels in the entire Yellowstone ecosystem.

Simulation runs were made for three cases: the upper and lower bounds on the population, and the most probable case. The simulations started with 1959 and continued until June of 1974.

Table 11—Percent known grizzly bear mortality by sex and age, 1959-1973

Age	*Male*	*Female*	*Unknown Sex*	*Total*	*% of Total Mortality*
Adults					
No.	75	62	9	146	
%	51.4	42.5	6.2	100.0	40.7
Sub-Adults					
No.	67	47	32	146	
%	45.9	32.2	21.9	100.0	40.7
Unknown Age					
No.	23	13	31	67	
%	34.3	19.4	46.3	100.0	18.6
TOTAL					
No.	165	122	72	359	
%	46.0	34.0	20.0	100.0	100.0

The lower bound is given by the simulation of the censused population that was shown in Figs. 6 and 7. This run would represent the ecosystem population if the census efficiency had been 100%. Our calculations show that it was not. Nevertheless, if state and federal agencies

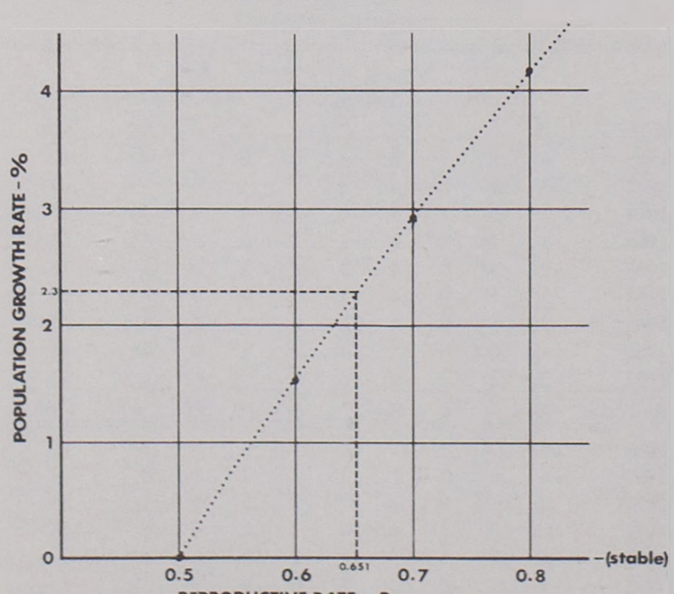


Figure 5.—Intrinsic growth rate of model vs. reproductive rate.

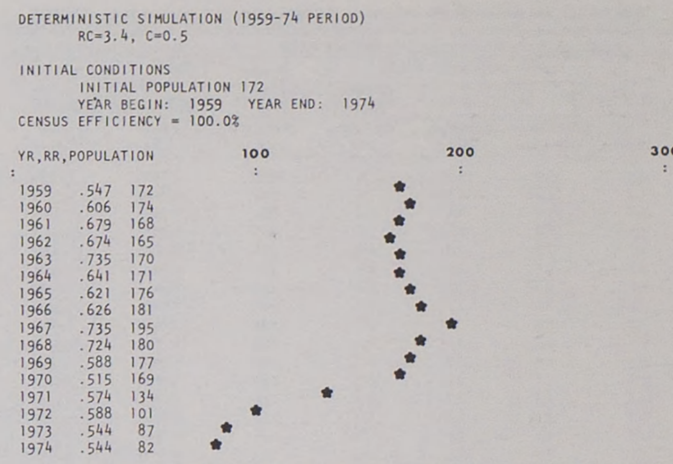


Figure 6.—Simulation run for censused population of grizzly bears.

wish to pursue fail-safe management for the grizzly, we believe they should base their hunting and control mortality allowances on this conservative estimate for the population level.

The upper bound on the population is given by assuming that the 40 deaths of unknown designation were all unmarked grizzlies. The census efficiency is then 177/318 = 55.7%. To make the simulation run, the starting population of Fig. 6 was scaled by the efficiency factor (172/0.557 = 309). Thus a population of 309 animals with an age and sex distribution proportionate to that given in Table 9 was used for the starting population. Since recorded mortalities represent a smaller fraction of this larger population, the correction factors for recorded mortalities used in the model were adjusted correspondingly.

The most probable situation is obtained by using the 77.3% census efficiency. For this case, the starting population was 172/0.773 = 222 animals, with appropriately adjusted mortality corrections (Fig. 8).

The results of these two runs are shown with the conservative lower limit in Fig. 9. For the optimistic case, the ecosystem population increases from 309 in 1959 to 334 in 1967, and then declines to 233 animals in 1974, a 30% decline. The population level remains constant at 233 for 1973 and 1974 with the assumed 1974 reproductive rate of 0.544.

The most probable case shows the ecosystem population increasing from 222 animals in 1959 to 245 in 1967, then declining to 136 animals in 1974. The population does not stabilize.

We conclude that the best estimate of the present grizzly bear population in the Yellowstone ecosystem is 136 animals. This best estimate demonstrates a 44.5% decline in size of that population from a high of 245 in 1967. Although recorded mortality levels have been lower during the last 2 years than in 1970-72, the population is still showing a decline with the reproductive rate observed in 1973. An increase in the reproductive rate or a further reduction of man-caused mortalities must occur before the population will stabilize. Even if reproductive rates eventually exceed mortality rates, recovery will be slow.

Table 12—Basic data for population model

1. *Total Starting Popolation* various (see text)
2. *Starting Population Age and Sex Structure* proportional to Table 9
3. *Cub Sex Ratio* (% male:female)

   *50:50

4. *Reproductive Rates*

1959—0.547	1967—0.735
1960—0.606	1968—0.724
1961—0.679	1969—0.588
1962—0.674	1970—0.515
1963—0.735	1971—0.571
1964—0.641	1972—0.588
1965—0.621	1973—0.544
1966—0.626	

5. *Recorded Ecosystem Mortalities*

Year	*MSA*	*MA*	*FSA*	*FA*	*Total*
1959	3	5	2	2	12
1960	7	6	6	5	24
1961	10	2	7	2	21
1962	4	2	6	3	15
1963	5	4	4	2	15
1964	6	3	2	1	12
1965	6	4	3	2	15
1966	7	3	2	1	13
1967	12	11	11	9	43
1968	5	9	2	5	21
1969	4	8	4	7	23
1970	13	13	14	13	53
1971	9	19	7	13	48
1972	5	10	4	8	27
1973	4	5	3	5	17

*Adjusted values

6. *Ratios of Recorded Mortalities to Total Population*

MSA	*MA*	*FSA*	*FA*
0.1212	0.1150	0.1180	0.0652

(based on average 1959-67 population of 178; factors scaled by census efficiency factor for simulations beginning with larger populations.)

7. *Survivorship Rates*

Age	*Males*	*Females*
0.5	*0.8000	*0.8000
1.5	0.6828	0.9529
2.5	0.8586	0.6790
3.5	0.8235	0.9091
4.5	0.5143	0.8200
5.5	0.9444	0.9756
6.5	0.9412	0.9500
7.5	0.9688	0.9737
8.5	0.9677	0.9730
9.5	0.9667	0.9444
10.5	0.9655	0.9706
11.5	0.9643	0.9394
12.5	0.8889	0.9032
13.5	0.8750	0.8571
14.5	0.7619	0.7917
15.5	0.7500	0.7368
16.5	0.8333	0.8571
17.5	0.8000	0.7500
18.5	0.7500	0.8889
19.5	0.8333	0.7500
20.5	0.8000	0.6667
21.5	0.7500	0.7500
22.5	0.6667	0.6667
23.5	0.5000	0.5000
24.5	0.5000	0.5000
25.5	0.0000	0.0000

DISCUSSION

We consider the decline in numbers of grizzly bears in the Yellowstone ecosystem to be serious for a species with a history of ecosystem and regional population extinction. The population history of the grizzly bear throughout its range in the United States has been characterized by gradual reduction in numbers, followed by apparent precipitous declines.

The evidence from this study demonstrates that the grizzly bear in the Yellowstone ecosystem has a low reproductive rate and that the population cannot sustain high mortality rates without threat to its integrity.

Improved fertility, following a decrease in population density, has been recorded for white-tailed deer (Cheatum and Severinghaus 1950), elk (Buechner 1955), coyotes (Knowlton 1972) and for other species. Therefore, as the bear population declines and the density decreases, one might expect the reproductive rate to increase above 0.544. However, the improved reproductive performance observed in herbivores and some carnivores has generally coincided with and been related to an improvement in nutritional level associated with better food conditions following population declines. We have no evidence that the Yellowstone grizzlies were stressed by food conditions at higher population levels. On the contrary, with a major food source removed (open pit garbage dumps) and with a learning process required to adjust to previously unexploited natural foods, the bears may have come under increased rather than decreased stress at lowered population levels.[3] Also, lowered density (Fig. 8) from 1:20,000 acres in 1967 to the most probable density of 1:37,000 acres in 1974 may decrease the opportunity to breed. The disruption of traditional spring movements and breeding patterns, caused by closure of the garbage dumps with abrupt decrease in available food, may keep the reproductive rate depressed for years. Thus we suggest that future management be based on a reproductive rate between 0.515 and 0.544 until conclusive scientific evidence shows an improvement in that rate.

The biological parameters we have obtained for the Yellowstone grizzlies show variability, indicating that the

[3]Craighead, J. J., J. Sumner, and F. C. Craighead, Jr. Food habits of grizzly bears in the Yellowstone ecosystem. (Manuscript in preparation for publication.)

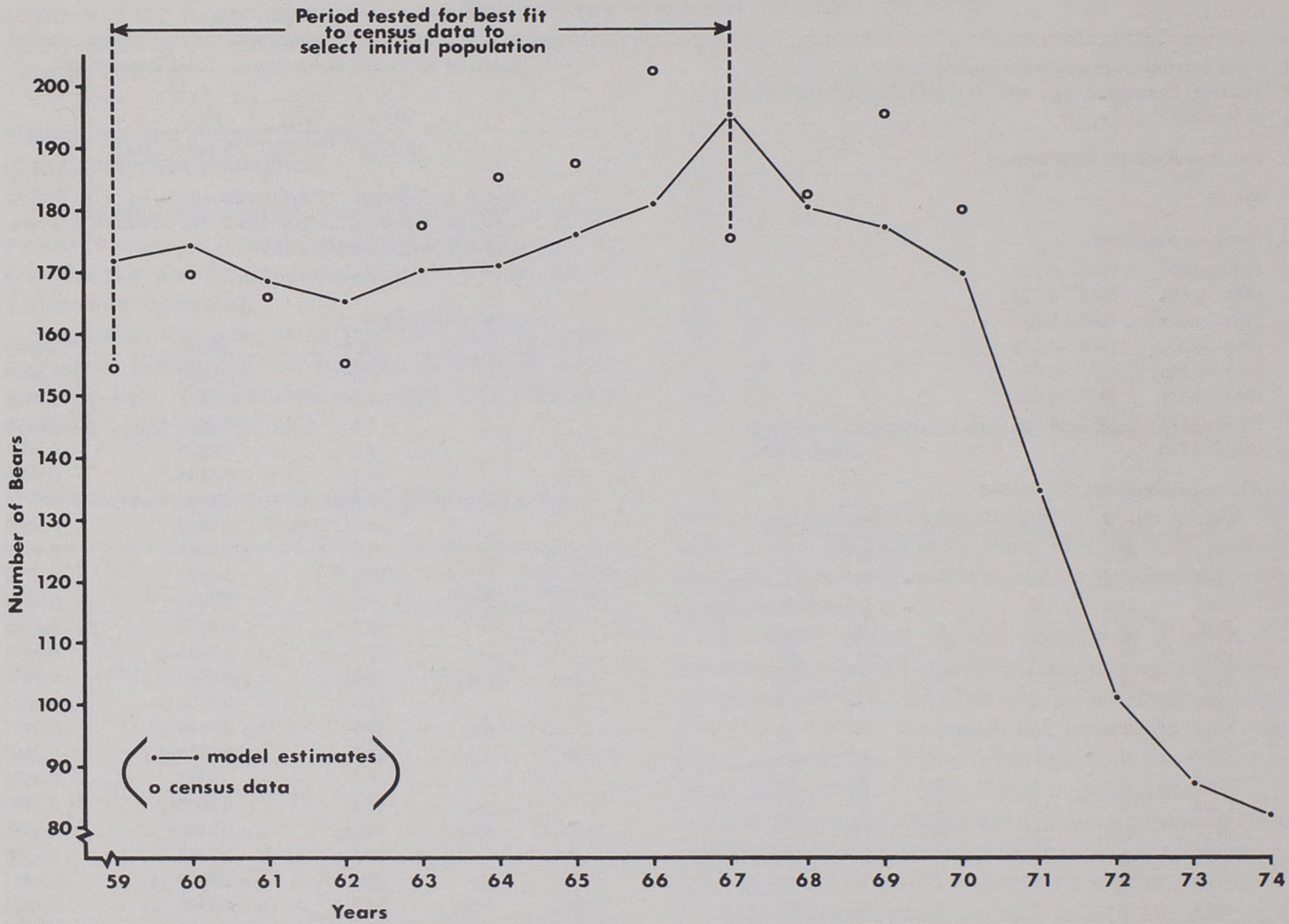


Figure 7.—Census data and population projections with model.

species, as we would expect, responds to environmental and physiological stresses. Under certain environmental conditions, now unknown, excessive adult mortality should be compensated by an increase in reproductive rate and survival of sub-adults. This would allow the population to grow, but to date there is no evidence that compensatory processes have yet become operative. On the contrary, our data and the history of grizzly bear populations since the early 1800's suggest that the species may respond very slowly in compensating for population declines or may be more limited than other species in its range of compensatory responses. The California grizzly *(Ursus arctos californicus)* and the cave bear *(Ursus spelaeus)* quite probably possessed population regulating

Table 13—Tabulation of marked and unmarked grizzly bear mortalities in the Yellowstone ecosystem, 1959-1970 (Note: Kill statistics from 1971 through 1973 were not utilized in the calculation because color marking of grizzlies by our research team ceased in 1970.)

	Yellowstone Park				*Surrounding Area*				*Total Mortality*			
Year	*No. Dying*	*Marked Dying*	*Unmarked Dying*	*Unknown Dying*	*No. Dying*	*Marked Dying*	*Unmarked Dying*	*Unknown Dying*	*No. Dying*	*Marked Dying*	*Unmarked Dying*	*Unknown Dying*
1959	8	5	3	0	4	1	3	0	12	6	6	0
1960	8	5	3	0	16	2	14	0	24	7	17	0
1961	9	7	2	0	12	5	7	0	21	12	9	0
1962	10	5	5	0	5	2	3	0	15	7	8	0
1963	9	5	4	0	6	2	4	0	15	7	8	0
1964	8	4	4	0	4	4	0	0	12	8	4	0
1965	7	4	3	0	8	4	4	0	15	8	7	0
1966	4	3	1	0	9	2	6	1	13	5	7	1
1967	11	7	4	0	32	1	4	27	43	8	8	27
1968	12	6	6	0	9	1	4	4	21	7	10	4
1969	12	7	5	0	11	2	9	0	23	9	14	0
1970	26	8	18	0	27	5	14	8	53	13	32	8
Total	124	66	58	0	143	31	72	40	267	97	130	40

Plate 5.—Adult males could be distinguished from adult females by their greater size, larger heads, and behavior, especially during the mating season.

mechanisms to strike an equilibrium between population density and the carrying capacity of their environments, yet the California grizzly became extinct about 1924 (Storer and Tevis 1955) and the cave bear did not survive beyond the end of the late Pleistocene (Kurten 1969).

The history of the species and the conclusions from this study suggest that agencies responsible for the preservation and management of grizzly bears must take a conservative approach to management. They should be extremely cautious in applying unproven management techniques and precise in controlling and harvesting the species. An informed approach to management in the Yellowstone ecosystem, based on long-term population statistics, is mandatory if a viable population is to survive.

Without color-marked or instrumented animals, it will be extremely difficult, if not impossible, to obtain accurate annual counts and sex and age designations of grizzly bears in the Yellowstone ecosystem. We are convinced that more accurate population estimates and trends can be obtained from simulations with the model than from field censusing of unmarked animals. Incorporating updated annual reproductive rates and known mortality records and compensatory responses, if identified, into the model each year will refine it into an increasingly precise, low-cost management tool.

```
DETERMINISTIC SIMULATION (1959-74 PERIOD)
     RC=3.4, C=0.5

INITIAL CONDITIONS
     INITIAL POPULATION 222
     YEAR BEGIN:  1959   YEAR END: 1974
CENSUS EFFICIENCY=77.32

YR.RR.POPULATION       100                 200                 300
:                        :                   :                   :
1959   .547  222                                *
1960   .606  223                                 *
1961   .679  217                               *
1962   .674  214                               *
1963   .735  219                                *
1964   .641  220                                *
1965   .621  225                                 *
1966   .626  229                                  *
1967   .735  245                                     *
1968   .724  231                                  *
1969   .588  228                                  *
1970   .515  218                                *
1971   .574  183                         *
1972   .588  152                   *
1973   .544  139                 *
1974   .544  136                *
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Figure 8.—Simulation run for ecosystem population of grizzly bears.

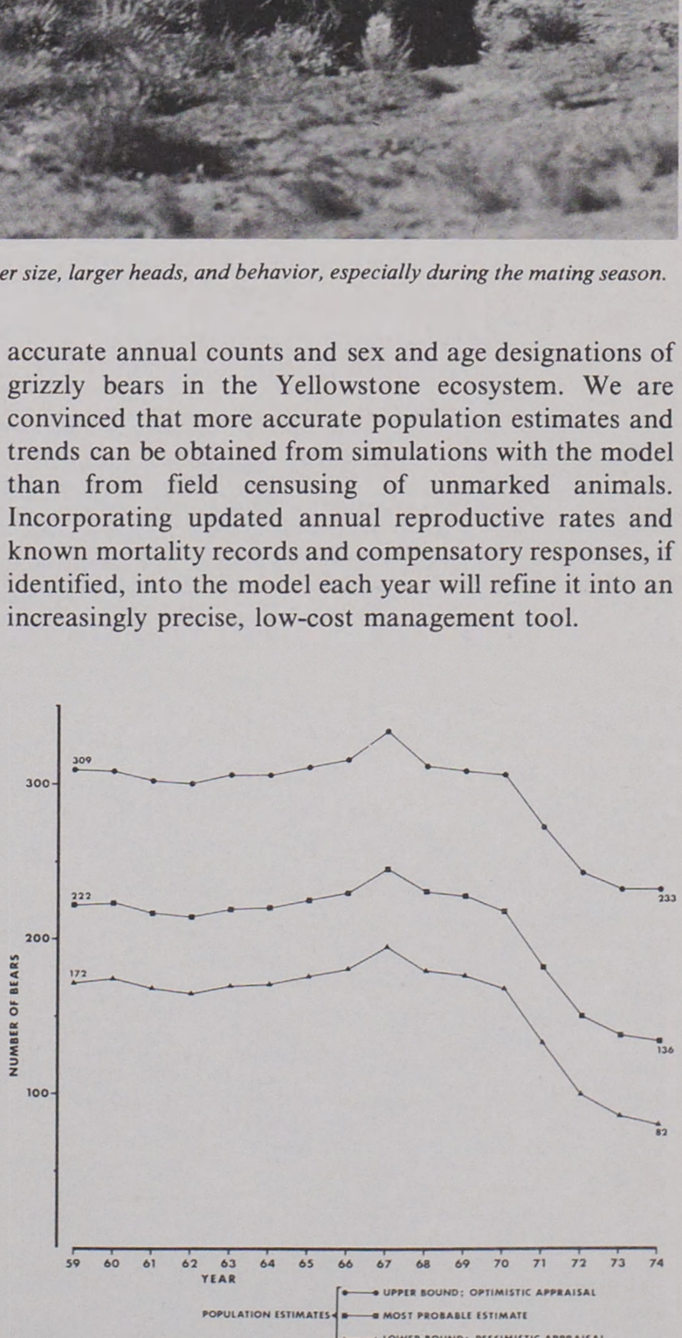

Figure 9.—Results of simulations of the grizzly bear population in the Yellowstone ecosystem.

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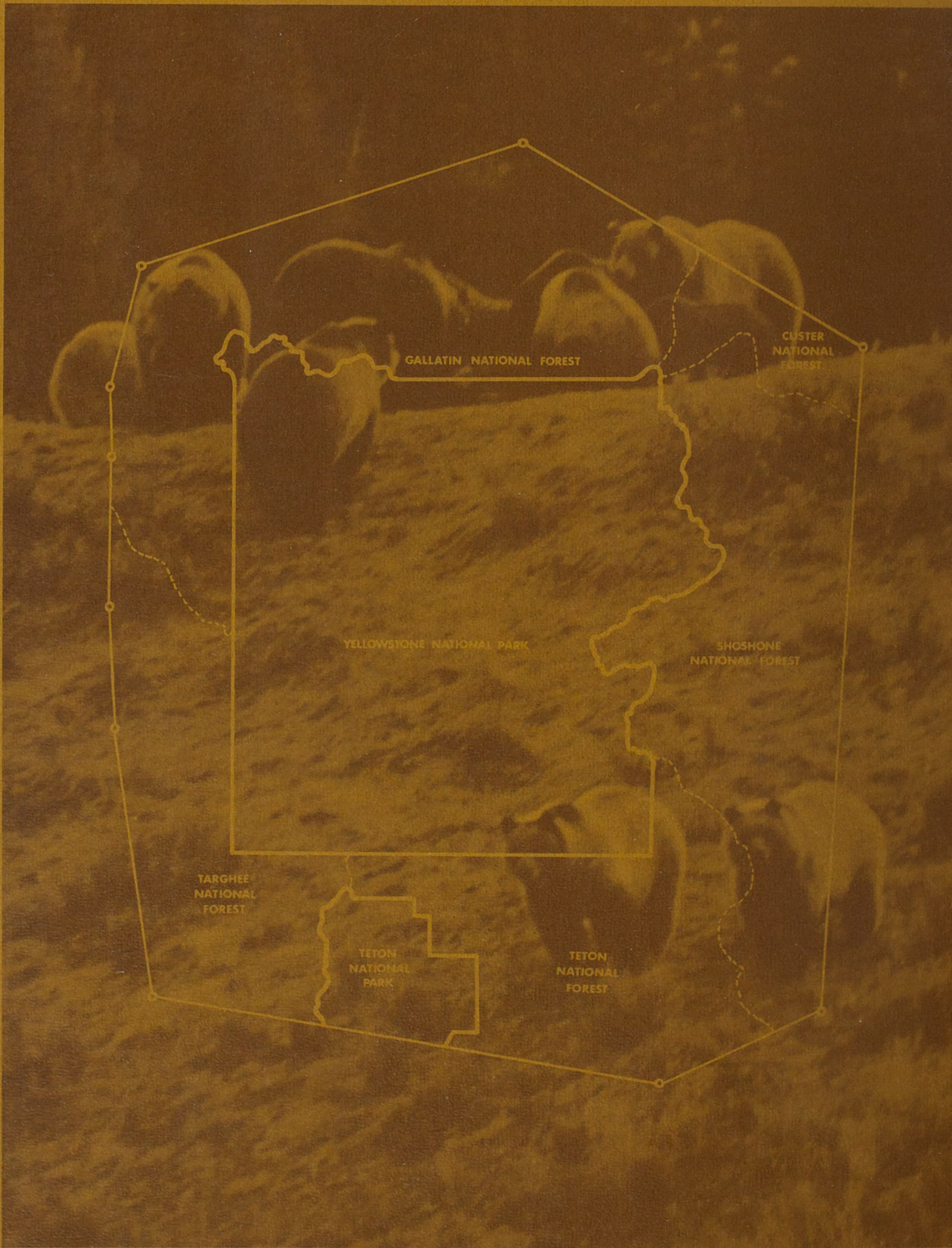
GALLATIN NATIONAL FOREST
CUSTER NATIONAL FOREST
YELLOWSTONE NATIONAL PARK
SHOSHONE NATIONAL FOREST
TARGHEE NATIONAL FOREST
TETON NATIONAL PARK
TETON NATIONAL FOREST