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POPULATION CHARACTERISTICS AND SOCIAL AND REPRODUCTIVE BEHAVIOR OF  
THE GRIZZLY BEAR IN YELLOWSTONE NATIONAL PARK

by

MAURICE G. HORNOCKER

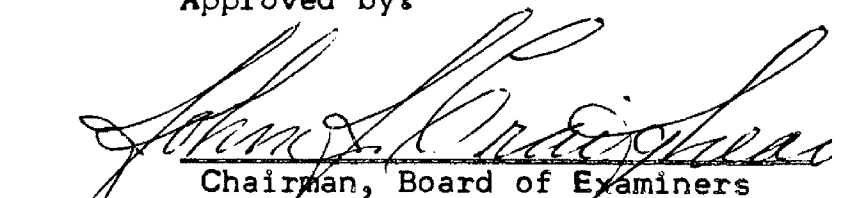
B. S. Montana State University, 1960

Presented in partial fulfillment of the requirements for the degree of  
Master of Science in Wildlife Technology

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Approved by:

  
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---

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M.G.H.

**PLEASE NOTE:** This dissertation is not a publication, and no portions herein may be quoted without express permission of the author and the Department of Zoology, Montana State University.

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## INTRODUCTION

Populations of grizzly bears (*Ursus arctos horribilis*) (Rausch, 1953) have been drastically reduced over much of their former range in the western United States. With the exception of Alaska, they now exist only as remnant populations in wilderness areas, national parks, and national forests of the Rocky Mountains (Craighead, et al., 1960).

Grizzlies have disappeared from Texas, New Mexico, Arizona, Utah, Oregon, Kansas and the Dakotas. In California, where they were once abundant, there has been no record of a grizzly since 1922 (Storer and Tevis, 1955). Cooney (1956) reviewed the status of the grizzly in the United States and concluded that the State of Washington may have a few, Colorado possibly 10, Idaho approximately 60, and Wyoming, excluding Yellowstone National Park, no more than 50. Montana lists about 450 exclusive of Glacier National Park. Estimates for Glacier and Yellowstone at that time showed 100 and 125 respectively. Rough estimates indicate the number of grizzlies left in the United States, excluding Alaska, may lie between 500 and 1,000 (Craighead, et al., 1960). There is need for detailed ecological studies of the grizzly if it is to be preserved and intelligently managed.

Such a long-term ecological study of the grizzly bear was begun in Yellowstone National Park in 1959. This study was initiated by the Montana Cooperative Wildlife Research Unit in cooperation with numerous other agencies. Yellowstone was chosen because it was found to have a

sizeable grizzly population and conditions were such that fundamental biological data could be obtained on a quantitative basis.

This paper deals with the first phase of the long-term study.

The primary objectives of this phase were:

1. To capture, mark, and release grizzly bears for future observations;
2. To determine population size and structure as a background for behavioral studies;
3. To observe and record behavior of individuals and family groups.

The population data were gathered throughout the Park but the behavioral studies were confined to the Trout Creek-Hayden Valley area.

Due to the joint efforts of many and the team approach so effectively utilized in this study, it is not feasible to sharply delineate all areas of work and responsibility. The research project was conceived and supervised by Dr. John J. Craighead and he worked closely with me both in the field and in the preparation of the data. The observations pertaining to population characteristics and the observations and interpretations on social and reproductive behavior presented in this paper are almost entirely my own. Many of the observations were duplicated and substantiated by other members of the research team but have not been included in the tabulations.

## THE STUDY AREA

### Geographic Location and Physiography

Yellowstone National Park lies in the northwest corner of Wyoming. An area 3,412 square miles in size, it extends into Montana and Idaho on the north and west (Figure 1).

The greater part of Yellowstone National Park is a high plateau lying approximately 8,000 feet above sea level. From this plateau many rugged peaks and ridges rise to altitudes of 10,000 to 11,000 feet. The valleys lie at 5,000 to 6,000 feet (Bailey, 1930). The Park is bordered by the Absaroka Range on the east, the Bear Tooth Range on the north, and the Madison Range on the west. The Absarokas extend into the eastern part of the Park and the Gallatin range reaches into Yellowstone from the northwest. Big Game Ridge and spurs from the Teton Range cross the southern boundary. Mountain ranges wholly within the Park include the Washburn Range and the Red Mountains. The Continental Divide crosses the southwest portion of Yellowstone in a northwest-southeast direction.

Yellowstone National Park gives rise to three major river systems, the Yellowstone, the Missouri (Madison and Gallatin Rivers), and the Snake. Extensive tributary systems of these rivers extend throughout the Park. Numerous lakes occur, the largest of these being Yellowstone Lake.

Extensive treeless areas, or valleys, occur in some portions of

Highway  
Bear Concentration Areas

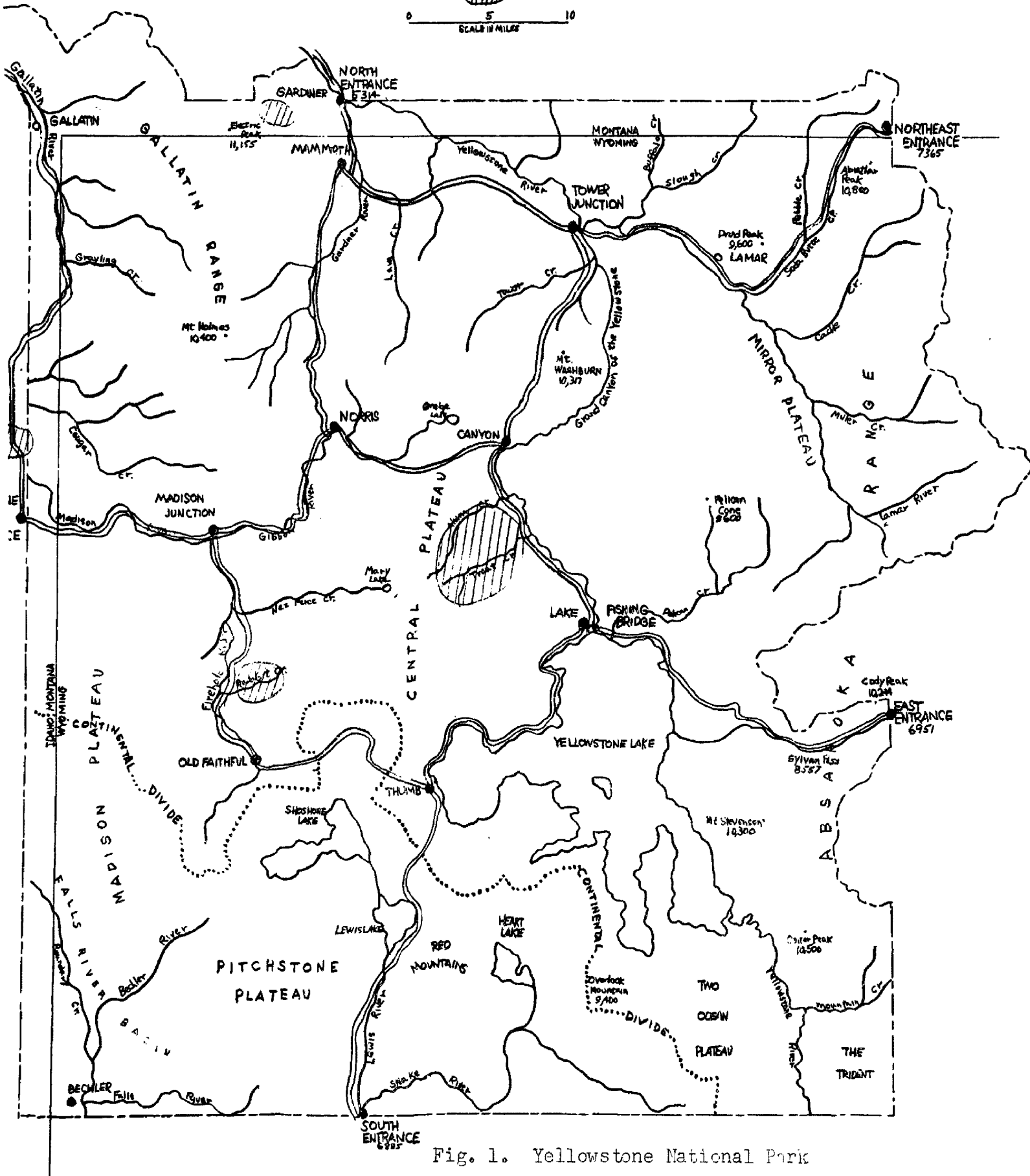
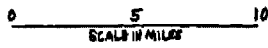


Fig. 1. Yellowstone National Park

the Park. The largest of these is the valley of the Yellowstone and Lamar rivers which is approximately 25 miles long and up to 10 miles wide. Other large valleys include Hayden Valley, in the central part of the Park; Swan Lake Flats, south of Mammoth Hot Springs; Elk Park and Gibbon Meadows, in west central Yellowstone; Pelican Creek Valley, east central; the geyser basins bordering the Firehole River, and areas around Shoshone and Lewis Lakes (Chittenden, 1905).

Although Yellowstone National Park itself is considered a plateau, several smaller plateaus are recognized within the Park. These plateaus range in mean elevation from 7,000 to 9,000 feet above sea level. Field investigations for this particular phase of the study were conducted primarily in the Central Plateau area.

### Climate

Temperatures average about 60° F. during the summer months in most areas of the Park (U. S. Dept. Commerce, 1959). The maximum rarely exceeds 80° F.; the minimum often is 30° F. or lower. In January, which is usually the coldest month, average temperatures range from near 0° F. at night to about 25° F. in early afternoon. Temperatures are frequently well below 0° F. and all areas of the Park have recorded at least -40° F., the record low being -66° F. near West Yellowstone.

Annual precipitation varies from an average of 13.73 inches at Lamar Ranger Station in the northeast portion to 38.26 inches at Bechler Ranger Station in the southwest corner. At the lower eleva-



tions, June is the wettest month with averages ranging from 2 to 3 inches. Daily precipitation of more than 1 inch is rare in the summer-time.

Snowfall is heavy over the mountains, averaging close to 150 inches annually, but in some local areas depths often reach 400 inches. While not common, there are records of several inches of snow in the summer months.

A summary of the weather data from 1930 through 1959, recorded at Park Headquarters, is presented in Table I. This station, lying 6,241 feet above sea level, is lower than most of the Park; consequently, average temperatures are somewhat higher and precipitation less than in other areas.

### Vegetation

Daubenmire (1943) lists six major zones of vegetation characteristic of the Rocky Mountains. These zones are distinguished by the nature of the climatic climax associations occurring at different elevations or in different regions. Three of these zones, the alpine tundra zone, the Engleman spruce-subalpine fir zone, and the Douglas fir zone, occur in Yellowstone National Park.

Alpine Tundra Zone. This zone occurs above timberline, which is at about 10,000 feet in Yellowstone. The vegetation that occurs in this zone in the Park fits Daubenmire's description of "alpine meadow" (Daubenmire, 1943). In this lower part of the alpine zone, the soil has become completely covered by a dense, low, meadow-like type of plant

TABLE I

SUMMARY OF AVERAGE MONTHLY PRECIPITATION AND TEMPERATURES RECORDED  
AT YELLOWSTONE NATIONAL PARK HEADQUARTERS FROM 1930 THROUGH 1959

Month	Temperature (°F)			Precipitation Totals (Inches)	
	Mean	Daily Max.	Daily Min.	Mean Precipitation	Mean Snow, Sleet
Jan.	18.0	27.2	8.8	1.10	17.7
Feb.	22.0	32.1	11.8	0.90	13.4
Mar.	27.0	37.9	16.1	1.27	16.3
Apr.	38.1	51.3	26.3	1.29	6.4
May	47.2	60.4	34.0	1.75	2.1
June	54.4	68.0	40.3	2.29	0.3
July	62.8	79.3	46.4	1.15	T
Aug.	61.1	77.5	44.7	1.32	T
Sept.	52.3	67.4	37.2	1.20	1.3
Oct.	42.4	55.0	29.8	1.16	4.7
Nov.	28.7	38.4	19.5	1.02	11.4
Dec.	22.4	30.9	13.8	1.11	14.9
Annual	39.8	52.1	27.4	1.30	7.4

cover. This cover is composed chiefly of grasses and sedges. Characteristic species include Carex spp., Phleum alpinum, Trifolium spp., Trisetum subspicatum, Festuca spp., Polygonum viviparum, and Potentilla spp. The sedges and grasses occurring in this zone are utilized by grizzly bears at certain seasons of the year.

Engleman Spruce - Subalpine Fir Zone. This zone usually occupies about 2,000 feet of elevation immediately below the alpine zone. This belt includes the greater part of Yellowstone National Park and is normally characterized by a climatic climax of Engleman spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa). In the past, fire has destroyed much of the climax spruce-fir association (McDougall and Baggley, 1956). In its place there has developed sub-climax forests of lodgepole pine (Pinus contorta) or aspen (Populus tremuloides). Bates (1917) states that lodgepole pine invades an area after fires of intense heat and aspen occurs after fires of moderate intensity. He also states that aspen invades the more mesic sites in areas of greater soil fertility. At the present time, lodgepole pine covers much of the Park and McDougall and Baggley (1956) believe that two or three fires each century are sufficient to perpetuate these stands. Aspen occurs mainly in the northern regions. Over the past 50 years, however, these aspen stands have been greatly altered due to overgrazing by elk. White-bark pine (Pinus albicaulis) also occurs in this zone, usually growing on higher ridges. The seeds of this species are important food items for bears.

Undergrowth in the lodgepole forests is characteristically scant and is dominated by Vaccinium scoparium, Arnica cordifolia, and Carex geyeri. Vaccinium membranaceum, although not common in Yellowstone, occurs in some of the more mesic sites. The vacciniums and sedges are important food plants for bears.

A number of "mountain parks" occur in this zone in Yellowstone, and are characterized by a sagebrush (Artemisia tridentata) - grass community. McDougall and Baggley (1956) believe that these parks were originally a detached portion of the Palouse Prairie similar to that of northern Idaho, and the present prevalence of sagebrush is due to overgrazing by elk. Daubenmire (1943), however, states that plant cover of these parklands is similar to that of the adjacent basal plains, and in the central Rockies sagebrush is dominant on the west slope. It is possible that this explanation applies to the Yellowstone area. Food plants utilized by bears in these parks include Heracleum maximum, Lomatium spp., Perideridia gairdneri, Cirsium foliosum, Camassia quamash, different species of grasses and sedges, and others.

Douglas Fir Zone. This zone occurs immediately below the spruce-fir zone and is characteristically dominated by Douglas fir (Pseudotsuga menziesii). This species is limited in Yellowstone, however, having been largely replaced by lodgepole pine, which maintains the same successional relationship to Douglas fir as it does to the climax forests at higher elevations. Aspen occurs in some areas. White-bark and limber pine (Pinus flexilis) grow on some of the wind-swept ridges.

Treeless areas also occur in this zone and support a sagebrush-grass sub-climax somewhat similar to that at higher elevations. Willow (Salix spp.) and sedges occur in more mesic sites.

### Fauna

Several species of large herbivores inhabit the Park. These include elk (Cervus canadensis), bison, or buffalo (Bison bison), moose (Alces alces), mule deer (Odocoileus hemionus), bighorn sheep (Ovis canadensis), and prong-horn antelope (Antilocapra americana). White-tail deer (Odocoileus virginianus), never abundant in Yellowstone, appear to have disappeared completely. Larger carnivores now inhabiting the Park are grizzly bears (Ursus arctos horribilis), black bears (Ursus americanus), and coyotes (Canis latrans).

Many different species of rodents and lagomorphs occur throughout the Park (Bailey, 1930). The principal carnivores utilizing these small mammal species are the badger (Taxidea taxus), marten (Martes americana), mink (Mustela vison), long-tailed weasel (Mustela frenata), and short-tailed weasel (Mustela erminea). Bobcats (Lynx rufus), skunks (Mephitis mephitis), and red fox (Vulpes fulva) are less numerous and are restricted to the lower elevations in the northern part of the Park. Lynx (Lynx canadensis) are rare, but have been reported in recent years. The wolverine (Gulo luscus) was never abundant in Yellowstone and none has been sighted in the past several years. The river otter (Lutra canadensis) is fairly common.

A great number of bird species utilize the diversified habitat

in Yellowstone. Some of these are year-round residents, but the majority nest here in summer and migrate each fall (Bailey, 1930).

Environmental conditions for the large mammals have changed since the Park was established in 1872. Populations of elk and bison have fluctuated with the changes in habitat. Wolves (Canis lupus) were exterminated in the 1920's because they were predators on the herbivores. The mountain lion (Felis concolor) reached near-extinction due to hunting; however, Park personnel report sightings of this animal in recent years. Coyotes survived early attempts to control their numbers and are now quite common.

Elk and bison supply a source of food for grizzly bears, largely in the form of carrion, but they appear to be of minor importance.

#### History and Description of Conditions

Both black and grizzly bears were probably no more numerous in Yellowstone in the late 1800's than in other areas of the northern Rocky Mountains. Early writers made infrequent reference to bears in the Yellowstone area. Skinner (1925) attributes the scarcity of bears in the Park to hunting, which was permitted until 1886. The Army assumed protection of the Park at this time and all shooting was stopped. By 1889, black bears had begun to frequent garbage piles and in 1890 had become so numerous that authorities considered reducing the population.

Grizzlies first began to feed at the refuse sites around 1893, but were quite wary (Skinner, 1925). The best available information

would indicate that the population increased through the early 1900's. No complete censuses were conducted, but Park personnel estimated 140 grizzlies in the Park in 1928 (Bailey, 1930). This figure rose to 320 in 1941, but became somewhat more realistic in 1950 when 180 were estimated (Condin, 1956).

It is the grizzly's inherent nature to scavenge and to congregate wherever food is available. Storer and Tevis (1955), quoting writers in the 1870's in California, speak of whale carcasses attracting a "regiment of bears" and of as many as 12 to 15 grizzlies feeding at one time on whale offal discarded by whaling crews. Bears in California also congregated to forage in wild pastures and in oak forests where acorns were plentiful. Grizzlies were observed ". . . feeding under oaks together. . . as composedly and as careless of danger as if they had been hogs. . ." (Storer and Tevis, 1955).

Lewis and Clark, in 1805, encountered large numbers of grizzlies along the Missouri River in what is now Montana (De Voto, 1953). The area upstream from the mouth of the Sun River was "infested with grizzlies" and in the vicinity of the Great Falls ". . . there were so many and became so troublesome that I (Lewis) do not think it prudent to send one man alone on an errand of any kind." Game was very abundant and Lewis estimated as many as 10,000 buffalo in a single herd. Although he does not mention bears feeding, he does speak of observing "vast many carcasses of Buffalow" in the river and of many animals in poor condition. One grizzly they killed was full of "flesh and fish." It appears that food for grizzlies was plentiful in this area. This,

and the fact that Indians were relatively incapable of killing them, probably explains the grizzly's abundance.

Troyer (1962) reports that Alaskan brown bears (Ursus arctos middendorffi) (Rausch, 1953) exhibit the same behavior in concentrating <sup>and</sup> on salmon streams/in berry patches on Kodiak Island. Here, 40 to 50 bears feed daily for a period of several weeks in an area of about one square mile.

The natural trait of bears to congregate where food is available appears to be intensified under the conditions prevailing in Yellowstone. In 1919, the National Park Service, recognizing this habit of bears, established feeding stations at Canyon and Old Faithful (Condin, 1956). This was done to enable Park visitors to observe bears at fairly close range. The danger posed by the grizzlies was realized and an armed guard was posted each evening. After the feeding stations were discontinued in 1941, many of the grizzlies accustomed to visiting these stations sought this food supply at the refuse dumps. Subsequent generations over the years have continued to concentrate at these sites.

At the present time, artificial food is available for a more extended period of time than is any one natural food source, with the exception of grasses, sedges, and other herbaceous plants. From mid-June to mid-September, food is available to the bears at the major refuse dumps. This tends to attract and hold bears in one general area for a longer period of time than does natural food alone. The extent that artificial food is utilized, as compared to natural foods, is not known with certainty. However, Skinner (1925) states "grass is



eaten as much, if not more than any other single item. . . bears do not depend upon garbage." Murie (1943, unpublished) studied the food habits of Yellowstone grizzlies and black bears and concluded that vegetation comprises 81 per cent of their food and garbage 6 per cent. Conditions have changed somewhat in the Park since these studies were conducted, and a food-habits study is currently underway to evaluate the influence of artificial food on the grizzly population. These preliminary investigations indicate that artificial food, while affecting dispersion and movement of the population, is not a major factor in governing total population numbers. Yellowstone affords a wealth of natural food; much of this is unused in favor of that obtained relatively easily at the refuse sites. The major factor believed to be responsible for sizeable grizzly populations in the Park is the protection afforded them.

The longer period of time and the season of year that the concentrations occur in Yellowstone may have altered the behavior of individuals within the population. The assertion of dominance is probably more pronounced under these conditions. Reproductive behavior may also be affected by concentrations occurring during the breeding season in June and July. However, Storer and Tevis (1955) report concentrations of grizzlies in "early summer," but make no mention of breeding activity. Lewis and Clark encountered large numbers of grizzlies in May and June in what is now Montana, and reported that copulation occurred at that time (DeVoto, 1953).

For purposes of this study, it is believed that the habit of

concentrating where food is available is inherent in grizzly bears and that the concentrations in Yellowstone are no more unnatural than those occurring in historic times or in Alaska today. Supplemental food supplies have affected dispersion and movement of the population, but are not considered a primary factor in determining population numbers; protection appears to be the major factor. The possibility is recognized, however, that a constant food supply from mid-June to mid-September may have altered some behavioral traits.

## METHODS AND TECHNIQUES

### Capturing

Grizzlies were captured in culvert traps mounted on trailer frames similar to those used by the U. S. National Park Service for capturing and moving nuisance bears. The basic design as well as trapping techniques were previously described by Erickson (1957), Black (1958), and Craighead, et al. (1960). Sets were made near feeding areas, along back roads, and occasionally outside isolated camp grounds.

One hundred fifty-seven grizzlies (initial captures and recaptures) have been trapped in these culvert traps by the research team since the start of the study in 1959 (Table II).

TABLE II  
METHOD OF CAPTURE, 1959-1961

Year	Total No. Bears Handled (Initial Capture and Recaptures)	Total No. Trapped	Total No. Shot Free-Ranging
1959	33	27	6
1960	64	56	8
1961	95	74	21
Totals	192	157	35

Trapping success for 1959, 1960, and 1961 is presented in Table III. On six occasions during 1961, failure of the trap to operate

properly lost bears that otherwise would have been captured. These six bears, had they been trapped, would have raised the trapping success in 1961 to 67.5 per cent, only 4.3 per cent below that in 1960. There is evidence, however, that some bears are becoming "trap-shy" and more difficult to capture.

TABLE III  
TRAPPING SUCCESS, 1959-1961

Year	Trap Nights	Successful Trap Nights	Per cent of Trapping Success
1959	21	14	76
1960	71	51	71.8
1961	77	46	59.6
Totals	169	111	65.7

In addition to those bears trapped, a number were "shot" free-ranging by injection of succinylcholine chloride using a propulsive syringe and gas-operated rifle (Craighead, et al., 1960). Thirty-five individuals have been captured in this manner (Table II).

Immobilizing and Anesthetizing

In 1959, succinylcholine chloride only was used to immobilize grizzly bears (Craighead, et al., 1960). During the summers of 1960 and 1961, succinylcholine chloride was again used to immobilize bears, but complete anesthesia was effected by the use of pentobarbital sodium similar to the technique described by Troyer, et al. (1961).

Marking

One hundred twenty-two grizzly bears have been captured and individually marked by the research team since the start of the study in 1959 (Table IV).

TABLE IV

SUMMARY OF BEARS INITIALLY CAPTURED AND MARKED, 1959-1961

Year	Total Number Marked	Age Class				
		Cubs	Yearlings	Two-Year Olds	Young Adults	Adults
1959	30	5	3	4	*	18
1960	47	6	5	4	9	23
1961	45	13	5	7	8	12
Totals	122	24	13	15	17	53

\* Young Adult category not used in 1959.

All bears except three were marked in both ears with aluminum cattle tags. In 1961, different colors were used in combinations and the tags were placed in the lower edge of the ear as well as the upper, or leading, edge. This was done to aid in identifying a bear should its color markers become lost.

With the exception of eight individuals ear-marked with polyethylene rope in 1960, all bears in 1959 and 1960 were ear-marked with polyvinyl chloride tape (Craighead, et al., 1960). In 1961, a number of bears were marked with Herculite, a nylon impregnated fabric, as well

as polyethylene rope and vinyl tape.

Adult males captured in 1961 were not color marked but were marked with metal ear tags only.

With the exception of a few bears, all were tattooed behind the foreleg or in the upper lip.

### Observations

The value of marked animals in a population being studied has been well demonstrated in the literature. A durable marker which is readily observable in the field makes this technique much more useful (Craighead and Stockstad, 1960). Life history data may be obtained without the necessity of laborious retrapping or sacrificing of animals. In addition, animals marked in this manner may be observed in their natural environment without disturbing them, and data obtained on certain types of behavior otherwise difficult or impossible to obtain.

The situation in Yellowstone, described in detail by Craighead et al. (1960), lends itself ideally to this technique. For approximately three months during the summer, large concentrations of grizzlies can be observed at four garbage dumps--Trout Creek, Rabbit Creek, Gardiner, and West Yellowstone. The behavioral studies were confined to Trout Creek. This site is located in Hayden Valley, a large treeless area near the geographical center of the Park. This area appears to be optimum summer habitat in Yellowstone. Bordering the vast Central Plateau, the region has remained essentially in a wilderness state. A great variety of plant foods are available in both wet and dry meadows,

as well as an abundance of berries in the surrounding lodgepole timber. White-bark and limber pine grow on nearby ridges and are a rich source of food in years of seed-cone abundance. The area supports large herds of elk and buffalo during the summer months and these contribute to the grizzlies' food supply. It is believed that this habitat is an important factor in attracting and holding the large number of bears that summer in this area. The fact that artificial food is also available is believed to supplement the natural environmental complex rather than to be a major factor in itself.

Environmental conditions at the other concentration sites are quite different from those in the Trout Creek-Hayden Valley area. These sites are located either in heavy timber or in areas where human disturbance is more frequent. Natural foods are also much less abundant than in Hayden Valley, and there appears to be no important difference in the amount of artificial food available at the four major sites. The numbers of grizzlies summering in these areas were considerably less than those in the Trout Creek-Hayden Valley area. Therefore, there appeared to be a direct relationship between bear numbers and the habitat surrounding the concentration sites, rather than a relationship between bear numbers and the amount of artificial food available. This appears to substantiate the belief that favorable natural environmental conditions were an important factor determining the larger population in the Trout Creek-Hayden Valley area.

Observations were obtained in two ways: (1) by observing bears at the concentration sites from a vantage point, and (2) by traveling

afoot in bear habitat in other areas of the Park.

Except in rare instances, grizzlies visited the concentration sites in the evening, remaining on into the night. Observations were made from a vehicle at the vantage point each evening. This vantage point was approximately 200 yards from the feeding site, but much of the activity was observed at a distance of 100 yards to 1/4 mile. A 7X50 binocular and a 20 power spotting scope were used for all observations. Bears were wary early in the season, but gradually became accustomed to the vehicle and ignored it. Meehan (1961) mentions similar behavior in Alaskan grizzlies--bears were apprehensive at first but soon paid little attention to humans in the area. The observer, frequently accompanied by other project personnel, usually took his position at the concentration site some time before the bears began arriving. The exact time bears arrived varied with climatic conditions, season of year, etc., but during June and July the first arrivals could usually be expected between 5:00 and 6:00 P.M. The observer ordinarily stayed until after dark.

In addition to those observations recorded at the concentration sites, a large number were made afoot in other areas of the Park. Bears were observed on kills, in bedding sites, and in areas where natural food was abundant.

Repetition of observations is necessary to obtain sufficient quantitative data on which to base interpretation and description of behavior. Special emphasis was placed on obtaining quantitative evidence of particular behavioral traits. The number of observations



recorded in this study on marked and unmarked but recognizable grizzlies and the number of different individuals observed for the three years are presented in Table V. A three-year total of 1,809 observations was made; 1,398 were of marked bears. Sixty-nine were obtained by re-trapping and 1,740 were direct observations in the field on free-ranging individuals and family groups. These observations were obtained on 179 different individuals and family groups.

TABLE V  
NUMBER OF OBSERVATIONS ON MARKED AND UNMARKED GRIZZLIES<sup>1</sup>

Year	No. Observations on Marked Bears	No. Different Individuals Observed	No. Observations on Unmarked but Recognizable Bears <sup>2</sup>	No. Different Individuals or Family Groups Observed
1959	160	13	-	-
1960	546	49	173	14
1961	692	86	238	17
Totals	1,398	148	411	31
Grand Total, Observations:	1,809			
Grand Total, Individuals:	179			

<sup>1</sup>Recognizable by scars, pelage color, family grouping, etc.

<sup>2</sup>Not recorded in 1959.

## Census

Censuses were made in three ways: (1) direct counts of marked and unmarked but recognizable individuals at the concentration sites, (2) counts of individuals in other areas of the Park, and (3) by aerial observations.

Direct counts were made at each of the concentration sites from early June through mid-September. These data yielded a minimum population figure for the Park. Scars, pelage coloration, and other characteristics of each unmarked bear and family group at the different concentration sites were recorded to avoid duplication. The numbers obtained by each count and the individuals involved were recorded and were compared to those obtained by previous counts. Movement of individuals from one concentration site to another in mid-summer was negligible and did not alter the counts.

Bears were widely dispersed in early spring and late fall, and a number were observed in areas far from the concentration sites. In no case was an individual added to the total count unless it was positively identified as a new individual.

Four flights were made in 1960 to test the feasibility of aerial counts and to check movement of bears. It was found that accurate counts could not be made from the air. Therefore, aerial censuses were discontinued.

## THE POPULATION

Storer and Tevis (1955), referring to the California grizzly, speak of large concentrations of these bears and of their seasonal migrations to areas where food was available. These areas included oak forests where acorns were plentiful, clover and grass meadows, and areas where berries were in good supply. Bears were gregarious at these concentration sites and as many as 40 were reported in sight at one time. Troyer (1962) mentions large concentrations of Alaskan brown bears on Kodiak Island. Here the bears are attracted by spawning salmon. Grizzlies in Yellowstone concentrate both in areas of natural food and at garbage disposal points, the larger and more easily observed concentrations occurring at the latter sites. Records obtained from marked individuals during the past three years show that grizzlies in Yellowstone travel great distances to these concentration sites. Many of these bears migrate from areas outside the Park, as well as from other areas within Yellowstone. Bears tend to return to these same areas in the fall.

### Population Buildup and Decline at Concentration Sites

In all three years, a gradual increase in numbers occurred at Trout Creek through June and July. The population appeared to reach its peak around August 1, followed by a gradual, then rather sharp decline in late August (Figure 2). The figures presented in Figure 2 represent the average for the three-year period and include only those

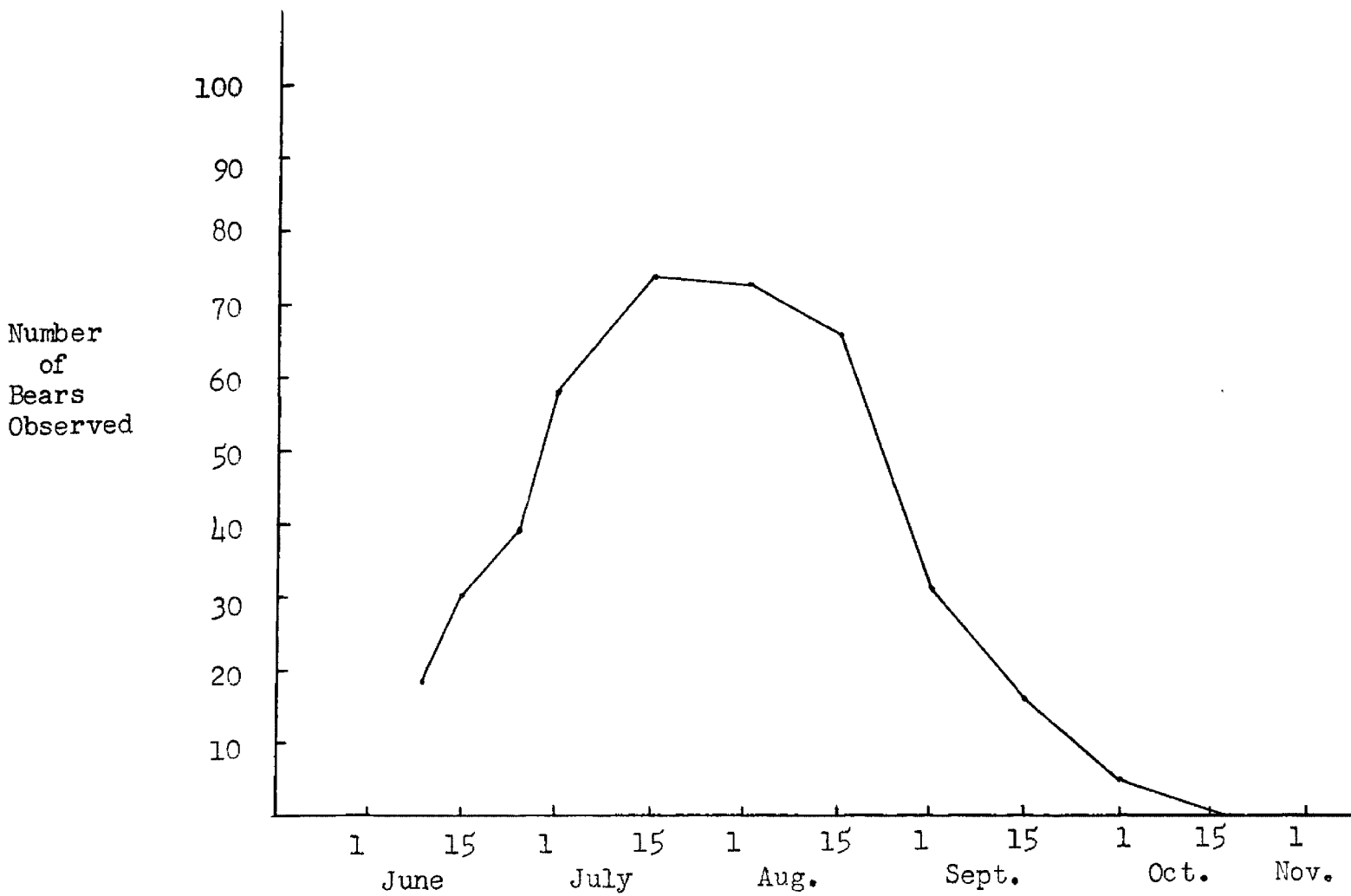


Figure 2. Population buildup and decline at Trout Creek, 1959-1961.

bears observed on the dates indicated. Not all marked or recognizable animals were present during a single count; these bears, however, were considered in arriving at the total population figure. This decline in numbers appears to be correlated somewhat with the amount of artificial food available at the refuse sites, but weather conditions and availability of natural foods appear to be equally important. In 1959, abundance of white-bark pine seed-cones appeared to have an effect on dispersal while relatively cold temperatures and frequent snows in 1961 initiated somewhat earlier movement from the summering area. In both these years, large quantities of artificial food was still available after dispersal had occurred. By mid-September, in all three years, only a fraction of the original peak number was still frequenting the area, and by mid-October, none.

The situation was basically the same at the three other major concentration sites.

### Census

Direct Counts. The number of direct counts made and the number of bears tallied at each site during the three-year period are presented in Table VI. These counts were conducted from early June through mid-September in all three years.

Table VI shows that the number of grizzlies counted at Trout Creek were remarkably similar for the three years. Counts at the other areas were less intensive and, in general, show greater fluctuation in numbers. It is believed that the counts closely represent the number of

TABLE VI  
GRIZZLY BEAR CENSUSES

Area	1959			1960			1961		
	No. Counts	No. Bears	Interval in Days Between First and Last Count	No. Counts	No. Bears	Interval in Days Between First and Last Count	No. Counts	No. Bears	Interval in Days Between First and Last Count
Trout Creek	17	96	98	24	98	91	31	98	90
Rabbit Creek	2	22	12	6	40	55	7	31	54
W. Yellowstone	2	27	12	3	16	50	4	19	54
Gardiner	2	9	24	2	9	31	2	10	25
Thumb	-	-	-	2	4	12	1	4	-
Pelican Creek Area*	-	-	-	-	2	-	-	4	-
Totals	23	154		37	169		45	166	

\* No counts made--bears trapped.

animals present, but the possibility exists that some bears were missed.

These direct counts show a minimum summer population of 154, 169, and 166 grizzlies in Yellowstone in 1959, 1960, and 1961 respectively.

Schnabel Method. The Schnabel Method of computing total population from sight-records of marked and unmarked animals (Schnabel, 1938) was applied to the Trout Creek data. The Trout Creek data were selected because this segment of the total bear population was intensively observed and contained a large number of marked bears. Only those marked bears observed in the area were considered in the calculations. Twelve of the 14 bears marked at Trout Creek in 1959 were observed in the Trout Creek area in 1960, and in addition 27 grizzlies were marked here in 1960. Thus 39 color-marked individuals were utilized in the calculations.

Twenty-three counts were made from June 16 to September 15, and these data are presented in Table VIIA. A mean population figure of 95, arrived at by the Schnabel Method, corresponds quite closely to the direct count number of 98.

Ten of the 14 bears marked in 1959 and 22 of the 27 marked in 1960 at Trout Creek were observed in 1961, and 32 more grizzlies were marked in 1961. Thus 64 marked individuals were utilized in the 1961 calculations.

Counts were made from June 9 to September 6, and a total of 29 counts were used in the calculations. These data are presented in Table VIIB. A mean population of 97 was obtained by this method and

TABLE VIIA

THE GRIZZLY POPULATION IN THE TROUT CREEK-HAYDEN VALLEY  
AREA AS DETERMINED BY THE SCHNABEL METHOD, 1960

Date	Total Bears Observed A	Bears Marked in 1960	Marked Bears in Area B	(A)(B)	$\xi(A)(B)$	Marked Bears Observed C	$\xi C$	Total $\xi(A)(B)$ $\xi C$
June 16	40	0	12	480	480	6	6	80
17	35	0	12	420	900	7	13	69
18	41	0	12	492	1,392	6	19	73
21	46	0	12	552	1,944	6	25	78
25	63	1	13	819	2,763	9	34	81
30	49	7	20	980	3,743	9	43	87
July 3	64	1	21	1,344	5,087	17	60	85
6	69	2	23	1,587	6,674	14	74	90
9	72	0	23	1,656	8,330	14	88	95
13	67	2	25	1,675	10,005	18	106	94
17	64	2	27	1,728	11,733	14	120	98
19	74	0	27	1,998	13,731	17	137	100
21	73	0	27	1,971	15,702	18	155	101
24	73	0	27	1,971	17,673	17	172	103
29	60	3	30	1,800	19,473	19	191	102
31	68	2	32	2,176	21,649	19	210	103
Aug. 5	66	1	33	2,178	23,827	18	228	105
12	70	1	34	2,380	26,207	21	249	105
15	71	0	34	2,414	28,621	22	271	106
17	77	0	34	2,618	31,239	22	293	107
25	61	2	36	2,196	33,435	21	314	106
Sept. 14	24	3	39	936	34,371	10	324	106
15	25	0	39	975	35,346	11	335	106
							Mean	95



TABLE VIIB

THE GRIZZLY POPULATION IN THE TROUT CREEK-HAYDEN VALLEY  
AREA AS DETERMINED BY THE SCHNABEL METHOD, 1961

Date	Total Bears Observed	Bears Marked in 1961	Marked Bears in Area	(A)	(B)	Σ(A)(B)	Marked Bears Observed	ΣC	Total Σ(A)(B) ΣC
	A		B	(A)	(B)	Σ(A)(B)	C	ΣC	ΣC
June 9	18	0	32	576	576	576	7	7	82
10	23	0	32	736	1,312	1,312	6	13	101
12	22	0	32	704	2,016	2,016	9	22	92
13	17	0	32	544	2,560	2,560	5	27	95
14	13	0	32	416	2,976	2,976	6	33	90
15	21	0	32	672	3,648	3,648	7	40	91
18	30	1	33	990	4,638	4,638	11	51	91
19	37	0	33	1,221	5,359	5,359	12	63	93
20	33	0	33	1,089	6,948	6,948	11	74	94
21	37	0	33	1,221	8,169	8,169	16	90	91
22	27	0	33	891	9,060	9,060	9	99	92
26	54	0	33	1,782	10,842	10,842	20	119	91
27	55	0	33	1,815	12,657	12,657	19	138	92
28	48	0	33	1,584	14,241	14,241	16	154	92
30	56	0	33	1,848	16,089	16,089	15	169	95
July 2	53	1	34	1,802	17,891	17,891	18	187	96
3	53	0	34	1,802	19,693	19,693	17	204	97
4	52	0	34	1,768	21,461	21,461	17	221	97
5	45	4	38	1,710	23,171	23,171	11	232	100
6	46	0	38	1,748	24,919	24,919	13	245	102
9	54	1	39	2,106	27,025	27,025	21	266	102
12	50	1	40	2,000	29,025	29,025	17	283	103
17	72	1	41	2,952	31,977	31,977	23	306	105
23	63	2	43	2,709	34,686	34,686	24	330	105
31	53	6	49	2,597	37,283	37,283	24	354	105
Aug. 6	58	3	52	3,016	40,299	40,299	28	382	105
17	52	7	59	3,068	43,385	43,385	26	408	106
26	60	1	60	3,600	46,985	46,985	34	442	106
Sept. 6	12	4	64	768	47,753	47,753	7	449	106
								Mean	97

is again remarkably close to the 98 obtained by direct count for 1961.

Equating the 1960 Trout Creek population figure of 95, obtained by the Schnabel Method, to the direct count figures for both Trout Creek and the Park-wide population, a calculated Park-wide population of 164 is obtained.\* This calculated figure closely approximates the direct count of 169.

If the 1961 data are similarly treated, the calculated Park-wide population figure is again 164. This also is remarkably similar to the direct count of 166.

Petersen Index. The Petersen Index, a method of computing total population from ratios of recaptured marked animals to initially captured unmarked animals (Petersen, 1896) was applied to the Trout Creek trapping data for both 1960 and 1961. The formula used in this method is:

$$P = \frac{MS}{R}$$

where: P = total population estimate.

M = number of animals marked and released, first trapping effort.

S = total number of animals captured, second trapping effort.

R = number of animals recaptured, second trapping effort.

Only those bears known to be in the area (observed or retrapped) were

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\* 95: X = 98:169      95 obtained by Schnabel Method at Trout Creek  
X = 164            98 obtained by direct count at Trout Creek  
                    169 obtained by direct count for Park-wide population

considered in the calculations.

Twelve bears marked in 1959 were present in the Trout Creek area in 1960. Five of these were retrapped in 1960. During the course of the season, 27 unmarked bears were captured and marked, making a total of 32 bears captured in 1960. Applying the Index formula to these figures, a population figure of 77 for 1960 is computed. This is significantly less than 98, the figure obtained by direct count.

In 1961, 10 bears marked in 1959 and 22 marked in 1960, for a total of 32, were present in the Trout Creek area. Twenty of these were recaptured in 1961. Thirty-two new individuals were captured and marked, making a total of 52 bears captured in 1961. Applying the Index formula, a Trout Creek population figure of 83 is obtained, again under the direct count figure of 98.

Different factors appear to be responsible for the smaller population estimate obtained by the Petersen Index method. The small number of animals worked with in 1960 is probably inadequate. In 1961, a number of recaptures were made selectively by immobilizing free-ranging bears. This could bias the results of this method. Therefore, the figures obtained by direct counts, and apparently substantiated by the Schnabel Method, are considered a more accurate determination of minimum population numbers in Yellowstone National Park.

### Structure

Age Composition Counts. Classification counts were made simultaneously with direct counts. The following age classes were distinguished:

Cubs of the year, yearlings, two-year olds, young adults, and adults. The distinguishing criteria were size, conformation, behavior, and to some extent pelage condition and coloration. Criteria similar to these were utilized for deer by Dasman and Taber (1956). In this study, marked known-age bears were available for comparison. In 1961 these included cubs of the year, yearlings, and two-year olds. Dasman and Taber point out, however, that no method applicable in the field will yield complete accuracy but that exercise of careful study at proper seasons will keep errors to a practical minimum.

Some difficulty was experienced, particularly during the first year, in classifying bears in the young age classes. There often is overlap in size of yearlings, two-year olds, and young adults and criteria other than size must be used. The inexperience of the observer in 1959 possibly affected the counts and some error may have been made in judging yearling and two-year old bears. It is believed that accurate judgment was made on yearling bears in 1960, but some two-year olds may have been classified incorrectly. Young adult bears were classified for the first time in 1960 and I feel that I was too conservative in classifying only 12 bears in this category. It is believed that, as nearly as is possible, the 1961 classification is accurate.

The age composition of the Trout Creek segment of the population for the three-year period is presented in Table VIII. This table shows the number of individuals present in each age class and the per cent of the total population that each class comprised. It will be seen that the percent composition of all age classes, with the exception of

two-year olds, remained relatively stable in each of the three years. The significantly lesser number of two-year olds classified in 1960 is unexplainable, but may be due to error in classification.

TABLE VIII  
CLASSIFICATION COUNTS, TROUT CREEK ONLY, 1959-1961

Age Class	1959	Per cent of Total	1960	Per cent of Total	1961	Per cent of Total
Cubs	18	18.8	20	20.4	18	18.4
Yearlings	12	12.5	11	11.2	9	9.2
Two-year Olds	15	15.6	3	3.1	11	11.2
Young Adults*	-	-	9	9.2	14	14.3
Adults	51	53.1	55	56.1	46	46.9
Totals	96	100.0	98	100.0	98	100.0

\*Young Adult category not used in 1959.

Table IX shows the classification counts made throughout the Park, including those made at Trout Creek, for each of the three years. It will be noted that the per cent composition for each age class in the total Park-wide population closely approximates that of the more intensively observed Trout Creek segment of the population.

The age composition found in each of the three years in Yellowstone (except for two-year olds in 1960) corresponds fairly closely with that found by Dean (1958) for grizzlies in Mt. McKinley National

TABLE IX  
CLASSIFICATION COUNTS THROUGHOUT YELLOWSTONE NATIONAL PARK,  
1959-1961

Age Class	Per cent of Total		Per cent of Total		Per cent of Total	
	1959	1960	1960	1961	1961	1961
Cubs	26	16.9	35	20.7	30	18.1
Yearlings	23	14.9	15	8.9	17	10.2
Two-year Olds	17	11.0	5	2.9	17	10.2
Young Adults*	-	-	12	7.2	23	13.9
Adults	88	57.2	102	60.3	79	47.6
Totals	154	100.0	169	100.0	166	100.0

\*Not classified in 1959.

Park. However, he reports slightly higher cub and yearling percentages. Erickson (1961), working with brown bear populations on the Alaskan peninsula, reports an age composition very similar to that found on this study. On Kodiak Island, the brown bear cub percentage very nearly approximated that of the grizzly in Yellowstone, but the per cent of yearlings and two-year olds in the population was significantly greater (Troyer, 1962).

In order to describe and interpret behavior, it is necessary to arrive at the age composition of the population. A detailed description of age classes as related to population dynamics will be treated in another paper.

Sex Ratios. The sex and age designation of bears captured and marked during the three-year study are presented in Table X. Fifty-eight males and 63 females, with one of undetermined sex, have been captured. This indicates, essentially, a sex ratio of 1:1.

The sex ratio in the cub, yearling, and adult classes remained almost exactly 1:1. In the two-year old and young adult categories, 32 individuals were captured, of which 12 were males and 20 were females. In view of the even ratios in the other age classes, particularly in the adults, it is believed that this difference is due to inadequate sampling of these classes.

TABLE X  
AGE AND SEX DESIGNATION OF MARKED BEARS, 1959-1961

Age Class	Males	Females	Total
Cubs*	12	11	24
Yearlings	7	6	13
Two-year Olds	6	9	15
Young Adults	6	11	17
Adults	27	26	53
Totals	58	63	122

\*Sex of one individual was not recorded.

## SOCIAL STRUCTURE AND BEHAVIOR

The growth, limitation, and survival of a population is related to behavior of its members through social and ecological organization (Scott, 1958). The effect of social organization upon a population varies from species to species and according to environmental situations. A highly organized social structure stresses survival of the population of rather than/the individual. In a poorly organized social structure, that is, one in which there is little organized cooperation between individuals, behavior is closely related to survival of the individual rather than to survival of the population. Varying degrees of social organization lie between these two extremes. An attempt was made in this study to determine the degree of social organization existing in the grizzly bear population and to interpret the significance of this structure.

### Dominance Hierarchy

Intraspecies dominance hierarchies based on aggressive-submissive interactions are of widespread occurrence among vertebrate animals both in the field and laboratory (Collias, 1950). These hierarchies reduce the amount of fighting among members of a population and are directly related to the well being of the individuals and, ultimately, to survival of the population (Tinbergen, 1953).

Among the Trout Creek segment of the grizzly population, dominance was vigorously asserted by a few of the larger adult males and a



definite "peck order" (Schjelderup-Ebbe, 1922; Collias, 1944) existed among these bears. The females and younger members of the population, in general, appeared to exercise dominance less forcefully against weaker and less aggressive individuals.

The general order of dominance at Trout Creek was arrived at by intensive observation. Dominance relations were studied by noting and recording each definite instance of aggressive-submissive interaction between given individuals. Twenty-three observation periods in 1959, 37 in 1960, and 34 in 1961, averaging 3 to 4 hours each and extending from early June through mid-September, were utilized in classifying bears in distinct dominance classes. These classes and the general order of dominance is depicted in Figure 3. This structure was essentially the same in all three years. Figure 3 also lists the number of individuals making up each class in 1961. Recognition of each individual is imperative in the construction of this type of order. Recognition of marked animals posed no problem; characteristics of unmarked individuals and family groups were checked and rechecked until the investigator felt that each was recognizable beyond doubt. The number of observations recorded during the three years on aggressive interaction of each dominance class is presented in Table XI. Only the more significant aggressive behavior was recorded. In some behavioral categories, interaction with all other classes was recorded; in others, interaction occurred with only a few of the other classes.

DOMINANT CLASS

Dominant Male  
Number 12

SUB-DOMINANT CLASS

Number XX

AGGRESSIVE CLASS

Aggressive Adult Males

<u>No. in Class</u>	<u>Specific Designation</u>
1	Cutlip

Aggressive Adult Females

<u>No. in Class</u>	<u>Specific Designation</u>
4	Nos. 34, 112, 120, Mother of Nos. 109 & 110

DEFENSIVE CLASS

Defensive Adult Males

<u>No. in Class</u>	<u>Specific Designation</u>
6	Nos. 14, 30, 33, 41, and 2 unmarked males

Defensive Adult Females

<u>No. in Class</u>	<u>Specific Designation</u>
7	Nos. 84, 119, Mothers of Nos. 94, 117, 98. Female with 2 yearlings & Female with 1 yr.

CAUTIOUS CLASS

Cautious Adult Males

<u>No. in Class</u>	<u>Specific Designation</u>
13	Nos. 46, 85, 87, 88, 111, 113, & 7 unmarked males

Cautious Adult Females

<u>No. in Class</u>	<u>Specific Designation</u>
12	Nos. 42, 44, 64, 75, 108, 7, 39, 65, 48, Mother of No. 29, & 2 unmarked females.

SUBORDINATE CLASS

Sub-Classes:

Young Adults

<u>No. in Class</u>	<u>Specific Designation</u>
14	Nos. 5, 10, 15, 32, 35, 40, 45, 74, 76, 81, 96, 101, Litter Mate of No. 32 & one unmarked member.

Two-Year Olds

<u>No. in Class</u>	<u>Specific Designation</u>
11	Nos. 6, 51, 115, 26, 95, 77, 29, 37, 38, 86, and one unmarked member

Weaned Yearlings and Orphans

<u>No. in Class</u>	<u>Specific Designation</u>
5	Nos. 43, 52, 53, 114, 78

Figure 3. Dominance classes and general order of dominance at Trout Creek, 1961.

TABLE XI

NUMBER OF OBSERVATIONS ON DOMINANCE INTERACTION OF DIFFERENT  
DOMINANCE CLASSES, 1959-1961

Dominance Class	Number of Instances Dominance Interaction Observed
Dominant Male	189
Aggressive Adult Males*	210
Aggressive Adult Females	203
Defensive Adult Males	256
Defensive Adult Females	202
Cautious Adult Males	141
Cautious Adult Females	130
Young Adults	133
Two-Year Olds	137
Weaned Yearlings	23
Orphans	18
Total number observations	1,452

\* Includes Sub-Dominant Male in 1961.

### Terms for Dominance Classes

A number of criteria were used in the separation of the dominance classes presented in Figure 3 and Table XI. Aggressive, defensive, and cautious are descriptive terms introduced as an aid in effectively characterizing classes and members within classes where adults are considered. Dominance, as it affected the whole population, was manifested in the adults, particularly those individuals at or near the top of the order. An effective classification of these individuals is imperative in the description of dominance interaction among adults of both sexes. These terms describe, in general, the behavior of a particular class and determine its level in the hierarchy. The behavior that these terms imply constitutes only a segment of the behavioral complex considered in defining the dominance classes. In each of the three dominance classes assigned to adults, the majority of animals classified met specified criteria, but some stratification based on aggressiveness existed within each class.

### Classification of Adult Males

Five distinct classes of adult males were recognized. These were the Dominant Male, Sub-Dominant Male, Aggressive Adult Males, Defensive Adult Males, and Cautious Adult Males. Only in 1961 was a Sub-Dominant class recognized and then contained only one individual. The major criteria used to separate these classes were aggressiveness, size, age, and in some cases a combination of all. Aggressiveness was the most important single factor determining the rank of the dominant

animal and members of the Aggressive Class. The males high in dominance rating exhibited definite aggressiveness in most of their activities as contrasted to a more submissive attitude exhibited by those of equal size and apparent age lower in the order. Scott (1958) suggests that experience--winning or losing an initial encounter and encounters thereafter--has much to do with the fighting ability of an individual and its social rank. Collias (1950) also states, ". . . there is evidence that this social rank is decided by fighting, bluffing, or passive submission at the initial encounter between any given pair of individuals, or by an early series of such encounters." These explanations are applicable to grizzly bear males.

The term aggressive is used to denote those males actually vying for the dominant position. These Aggressive Males hesitated to retreat before the Dominant Male, and in rare instances, actually sought combat with him. All other members of the population were subordinate to this class of males. An exception was the bear which was assigned to the Sub-Dominant class in 1961. This male exhibited a greater degree of aggressiveness toward all others than did any of the other Aggressive Males. His behavior in this respect paralleled that of the Dominant Male.

Those males that avoided the dominant animal and those immediately subordinate to him were classified as Defensive Males. They fought with individuals higher in the structure only when surprised, cornered, or attacked. All members of the population below them in the order were subordinate to this class.

Cautious Males avoided, when possible, any contact with those individuals more aggressive than they. They escaped encounters by retreating on the run. Only on rare occasions were the members of this class actually forced to fight. These males exercised dominance over all members lower than themselves in the order.

#### Classification of Adult Females

The same designations applied to adult males--aggressive, defensive and cautious--were equally applicable to adult females. Criteria used to classify the females were aggressiveness, reproductive condition, age and size, and a combination of all in some instances. As in the males, aggressiveness appeared to be the one most important factor determining the status of individuals and the respect accorded them by other members of the group. The females' position in the dominance structure differed from that of the males. The dominance rank of adult males remained relatively unchanged with respect to one another. In contrast, the females' social rank, in relation to adult males, was temporary, while their status with respect to all other bears was relatively stable. Aggressiveness, plus the phase of the reproductive cycle, appeared to be the major factors governing the females' behavior toward adult males. Aggressiveness, size, age, or a combination of all, determined the adult females' social rank in relation to members of the population other than adult males. Reproductive condition had little effect on dominance behavior toward these lesser individuals.

Females with cubs of the year were subordinate only to the Dominant Male and those males immediately under him and were classified as Aggressive Females. They readily attacked any male, including the Dominant Male, that approached them or their offspring too closely. These females were extremely watchful over their young, constantly tending them while the family was in the concentration area. They excitedly drove or urged their cubs away when an adult male approached. Most displayed strict disciplinary action over their cubs.

Females with cubs of the year and females with yearlings that avoided, when possible, conflicts with superiors were classified as Defensive Females. They would fight only when pressed too closely. They were not so watchful of offspring as were the Aggressive Females, nor did they demand the same degree of obedience from their offspring.

Cautious Females were those females with no offspring. Behavior varied within the class, but in general, the members of this class displayed submissive behavior toward more aggressive individuals higher in the structure.

#### Adult Male - Adult Female Interaction

The position of the adult males in the overall dominance structure remained basically the same each year. There was some shifting of individuals near the top of the order, but adult males in all classes were involved in a yearly struggle for dominance. With some, this struggle was limited to conflicts with those within their particular class and with those members of the population below them. Among

the more aggressive males, conflicts also occurred frequently with superior individuals. Massive wounds and scars on the heads and necks of some indicated the severity of some of these fights. Ears were mutilated and often completely torn off of many of the older males, and many of them had torn and scarred lips and jaws.

Adult females held a somewhat different position in the hierarchy. Their social rank in relation to individuals other than adult males remained, as indicated earlier, relatively unchanged each year. They exerted dominance over lesser individuals less forcefully than did the males, and serious combat seldom occurred. The position of females high in the order was temporary. Near the top of the dominance structure, interaction occurred with adult males, and this was governed by the females' reproductive condition. Therefore, each year individual females displayed somewhat different behavior toward adult males because their reproductive status had changed. Thus an Aggressive Female one year could become a Defensive Female the following year, providing she retained her offspring. The next year, after weaning the young, her behavior would change again and she would be characterized by cautious behavior and thus be classified as a Cautious Female. Table XII shows the change in behavior, and thus the change in dominance class, of five adult females toward adult males during the reproductive cycle. It will be seen that the females' reproductive status--whether they had cubs, yearlings, or no offspring--had a direct bearing on their behavior toward the males. This change in behavior of the females was consistent throughout the Park-wide population, but



TABLE XII

CHANGE IN DOMINANCE CLASS OF FIVE ADULT FEMALES AT TROUT CREEK,  
BASED ON BEHAVIOR TOWARD ADULT MALES DURING THE REPRODUCTIVE CYCLE

Female	Dominance	Dominance	Dominance	Reproductive Status		
	Class in 1959	Class in 1960	Class in 1961	1959	1960	1961
No. 7	Aggressive	Defensive	Cautious	With Cubs	With Yearlings	Offspring Weaned
Mother of No. 26	Aggressive	Defensive	Cautious	With Cubs	With Yearlings	Offspring Weaned
Mother of No. 29	Aggressive	Defensive	Cautious	With Cubs	With Yearlings	Offspring Weaned
No. 39	Aggressive	Cautious	Cautious	With Cubs	Offspring Weaned	No Offspring
No. 65	Cautious	Aggressive	Cautious	No Off- spring	With Cubs	Offspring Weaned

only those females observed intensively at Trout Creek are presented in Table XII.

Fights with males were often furious, but ordinarily of short duration, and females showed none of the characteristic battle scars of the males. Females with offspring did command enough respect from adult males to warrant equal rank with some adult males in the dominance structure. These specific relationships will be discussed under each class.

#### Classification of Younger Bears

Young bears were recognized as having behavior sufficiently

distinct from adults to warrant being placed in a separate dominance class. Accordingly, they were assigned to the Subordinate Class. Bears within the class were classified in sub-classes: Young Adults, Two-year Olds, and Weaned Yearlings-Orphans. These three sub-classes comprised the lower segment of the dominance order. There were individuals in the Young Adult and Two-year Old sub-classes, however, that displayed unusual aggressiveness. These bears often exhibited threatening behavior toward both adult males and females. In general, the behavior of bears in these sub-classes toward superior individuals was submissive.

Size and age were the major criteria used in the classification of Young Adults. The members of this class displayed a much wider range of aggressive-submissive interaction than did those in any other class. This behavior varied from those who were relatively aggressive toward all members of the population to those who were apparently afraid of all others. In general, however, the behavior of the members of this class toward superior individuals was basically the same.

Two-year Olds were also classified by size and age. In many respects, their behavior was similar to that of the Young Adults. Bears in this category running with litter mates held a somewhat stronger position in the social structure than did lone individuals.

Weaned Yearlings and Orphans were the lowest members in the dominance structure. Their numbers were small in relation to others and they were physically inferior. This was undoubtedly a factor in their status. The fact that they were "cast-offs," however, with no family ties, appeared to be the major factor determining their social position.

Bears were classified as Orphans only when it was known that the mother had been killed. The members of these two classes were apprehensive of all other bears.

## DOMINANCE BEHAVIOR

### Dominant, Sub-Dominant, and Aggressive Adult Males

The Dominant and Sub-Dominant Males and Aggressive Adult Males were the ruling classes in the Trout Creek hierarchy. Each of the first two classes consisted of a single male; the Aggressive class was made up of two to four members, the number varying each year. These classes were characterized by a definite "peck order," the Dominant Male holding the top position. This position of dominance was gained by actively seeking combat with and defeating Aggressive Males. The most aggressive of these and the most consistent challenger of the Dominant Male was the Sub-Dominant Male. Dominance, once firmly established, was then asserted vigorously over all other members of the population, and the Dominant Male commanded respect from all others. This respect was evident by the response of individuals to the Dominant Male--a simultaneous, mass response of all animals present. Individuals lower in the structure responded to the Dominant Male's approach by becoming alert and scattering in confusion; Aggressive Males and Females respected his presence, but to a somewhat lesser degree. Aggressive Females did not hesitate to attack the Dominant Male when he approached too closely but invariably they were driven off. Aggressive Males usually attempted to bluff or to avoid completely the Dominant Male, but occasional fights did occur. The dominant animal was particularly aggressive toward these males.

Aggressive Males enforced respect from all lesser individuals, but not so forcefully nor so consistently as did the Dominant Male. They did not, in general, elicit the mass response from others that characterized the Dominant Male's relation to all members of the population.

Establishment of Individual Dominance. Two very large males were vying for the position of dominance when observations began in June, 1959. Both these males appeared old, were badly scarred, and thus readily recognized. "Scarface" had massive scars on both sides of the face and head, and the left ear was completely torn off; "Cutlip" was also badly scarred about the head, and a large portion of the lower lip was torn free and hung down loosely, exposing the teeth. These males never became involved in an all-out struggle, at least while I was present, but they did have several skirmishes. Much bluffing, accompanied by bawling and roaring, usually preceded these skirmishes. This bluffing alone, in the form of threatening postures, often was the only aggressiveness displayed. By July 1, Cutlip, the slightly larger of the two, had gained superiority. These two males did not limit their hostility to each other--all the others, including adult males, recognized their superiority and hastily avoided them.

On July 6, 1959, another large male appeared for the first time. This bear looked to be somewhat younger and was slightly smaller than either of the two old males. This new bear, upon arriving at the concentration site, made directly toward Cutlip, the dominant individual.

Cutlip fled without giving battle. The new-comer then turned and approached Scarface, who turned to meet him, and they rushed together, roaring and biting. The new bear was definitely the superior fighter, and soon Scarface also fled. The new-comer then proceeded to chase every adult male in the area. From that time on this bear, later to become Marked Bear No. 12, was unquestionably the dominant animal at Trout Creek.

It is believed that the new bear - Number 12 - assumed the dominant position for the first time in 1959. As previously stated, members of the population below the level of Aggressive Males and Females became alert and ran in confusion at the approach of the Dominant Male. This was the reaction early in 1959 to the approach of either Scarface or Cutlip. When Cutlip had gained some superiority over the other, this mass reaction was limited to him. After being replaced by the new bear, Cutlip was relatively ignored, while Number 12, now dominant, elicited this reaction and continued to receive the respect of all bears through 1960 and 1961. At no time during the three-year study did another male elicit such intense, mass response, with the possible exception of the Sub-Dominant Male in 1961. Others assumed temporary dominance in the absence of Number 12 but their superiority, judged by the reaction of others, did not approach that of this animal. Therefore, on the basis of these observations, I believe the old males recognized Number 12 in 1959 from previous years' encounters, and for the first time he was successful in his bid for dominance.

Number 12 retained the position of dominance throughout the

three years. The aggressiveness with which he maintained his position varied somewhat with season of the year, reaching its peak during the breeding season. At this time, he was extremely pugnacious toward all other individuals, regardless of sex, age, or size. This will be discussed more fully under Reproductive Behavior. His aggressiveness, however, toward those Aggressive Males immediately subordinate to him remained at a relatively high level throughout the season. The intensity of dominance, directed toward individuals other than males high in the order, changed drastically immediately after the last observed breeding activity (July 6, '59; July 10, '60; July 10, '61). Number 12 displayed this drastic and abrupt change in behavior each of the three years. On the dates indicated, he was fiercely aggressive toward all individuals; the following evening, his behavior completely changed. He showed little or no aggressiveness toward those classes below the Aggressive Males and this behavior pattern continued throughout the rest of the season.

No other male seriously threatened Number 12's position during the three-year study, although several attempted with varying degrees of vigor. The males that actually appeared to seek the role of dominance are listed in Table XIII. Characteristic names or numbers were given each unmarked individual. Table XIII lists the number of times that actual fighting or bluffing was observed between any two of these males. "Fighting" means that actual physical combat occurred; "bluffing" means posturing, chasing, and other aggressive-submissive behavior where no physical combat was involved. It will be seen in Table XIII that

TABLE XIII

BEHAVIOR OF DOMINANT, SUB-DOMINANT, AND AGGRESSIVE MALES; TO ESTABLISH DOMINANCE  
1959-1961

Males	Domi- ance Rating	No. Actual Fights		No. Bluffs		Victory, Fights		Victory, Bluffs		Per cent Success, Fighting & Bluffing	
		With Dom. Male	With Other Males	With Dom. Male	With Other Males	With Dom. Male	With Other Males	With Dom. Male	With Other Males	With Dom. Male	With Other Males
Number 12	1	1	14	0	34	1	14	-	34	100	100
Number XX	2	7	3	3	6	0	3	0	6	0	100
Cutlip	3	3	0	0	5	0	-	-	4	0	80
Scarface	4	2	0	0	5	0	-	-	3	0	60
Number 73	5	2	0	0	3	0	-	-	3	0	100



the Dominant Male was 100 per cent successful in both fighting and bluffing. It should be understood that this table is a composite form; Cutlip and Scarface were most active in 1959, Cutlip, Number XX, and Number 73 in 1960, and Number XX alone in 1961. The Dominant Male fought with others a number of times, but these four individuals appeared to be the real challengers for his position.

Number XX has been given the Number 2 position in the dominance hierarchy because he appears to be the present contender. In 1961, this bear exhibited sufficient dominance to warrant classification in a separate Sub-Dominant class. Although present as a recognizable individual in 1960, he did not gain any noticeable superiority over the other contenders until 1961. A younger appearing male, he was quite reluctant even in 1960 to back down from the Dominant Male. A number of times during the course of the season the following sequence occurred: Number 12 would make bluffing charges at Number XX, never carrying the charge through. The latter would crouch in a defiant manner, facing Number 12 and roaring loudly. The two would eye one another for a time, then invariably the Dominant Male would turn and resume other activity and the challenger would do the same. This procedure was often repeated two or three times. After attempting several such bluffs, Number 12 would suddenly, and quite unexpectedly, charge into the other at full speed. On several occasions, the younger male was bowled completely over. The Dominant Male would then press the attack, lunging and striking straight forward with the forefeet. He seldom tried to close

with the other and bite, which was always the case in more serious fights. Number XX would crouch low, facing Number 12, countering the latter's lunges with lunges of his own but always backing away slowly. The two never took their eyes off each other and both howled and roared continuously. Number 12 would press steadily on after each lunge, backing the other farther away. This continued for some time, and perhaps a distance of 100 yards, then the Dominant Male invariably would turn away for a moment. The younger male would always take this opportunity to whirl and run in retreat. Number XX would eventually return, but was cautious and watchful of Number 12.

This was essentially the pattern of behavior between these two individuals early in 1961. However, as the season progressed, the younger bear appeared to gain confidence and become more aggressive, particularly toward lesser individuals. His behavior in this respect paralleled that of the Dominant Male. On July 9, he entered the concentration area and made directly for Number 12. Number 12 went out to meet him, they roared and leaped together, striking out with the forefeet and biting at each other. The fight did not last long, and Number 12 prevailed. He did not press his advantage, however, and Number XX remained in the area. Both were extremely intolerant of any other bear, with the exception of a female apparently in estrus. This was the only occasion where it appeared that Number XX was eager to fight the Dominant Male. Fights did occur later, but were always instigated by Number 12. Number XX did assume a much stronger position in the hierarchy in 1961 as far as all others were concerned. In the absence of Number 12,

he assumed the dominant position and vigorously displayed his dominance. He, like Number 12, was quite aggressive toward other adult males, particularly those in the Aggressive and Defensive classes.

None of the other males in Table XIII were so aggressive toward the Dominant Male as was Number XX, nor were they so intolerant of lesser individuals. They did, however, assume the position of dominance when Number 12 was not present. When the Dominant animal arrived, they gave up the position, usually without a fight. Cutlip's position has remained about the same since being replaced by Number 12 in 1959, except that Number XX was definitely superior to him in 1961. Scarface, a very old appearing bear in 1959 and 1960, did not appear in 1961, and may have died. Number 73, in the absence of others, was dominant at Trout Creek early in 1960. Number 12 replaced this male shortly after he arrived. Like Scarface, Number 73 did not appear in 1961.

The Dominant and Sub-Dominant males and Aggressive Males were intolerant of all other individuals below themselves in the order, with the exception of Aggressive Females. These females would rush to challenge any of the males high in the dominance structure, including the Dominant Male, when they approached them or their offspring. In general, the males tended to avoid these females, and when actually attacked, usually would not fight vigorously and would slowly retreat. An exception was Number 12, and Number XX in 1961. Number 12 seldom went out of his way to avoid an Aggressive Female and fought back furiously when attacked. On August 3, 1959, however, he was attacked unexpectedly and simultaneously by two Aggressive Females and administered some apparently

painful wounds. For several evenings after this encounter, he carefully avoided those two particular females. This behavior lasted for five days; he then became as domineering as before. Number XX, in 1961, displayed this same intolerance of Aggressive Females.

### Defensive Adult Males

Defensive Males ranked just below Aggressive Males. They avoided the Aggressive Males when possible but would fight when surprised or cornered by a superior individual. Members of this class often equaled the Dominant Male and Aggressive Males in size, but in general, appeared to be younger. There was no order of dominance within this class, and only occasionally did fighting occur. They were more tolerant of lesser individuals, never appearing to assert their dominance over others in the manner of the Aggressive Males. They ranked on a level with the Aggressive Females, as far as the entire hierarchy was concerned, but definitely avoided these females. When attacked by the females they invariably retreated.

### Cautious Adult Males

These males were smaller and generally appeared younger than either Aggressive or Defensive Males. Aggressiveness varied somewhat within the class but their behavior toward others in the hierarchy was basically the same. Assertion of superiority was limited to those classes below them in the structure.

### Aggressive Adult Females

Aggressive Females held their position in the hierarchy because of their relationship with adult males. While their dominance over individuals below them in the structure was exerted much less forcefully than was the males', the degree of their hostility toward adult males often exceeded that of the males themselves. Their relative disregard for the superiority of some adult males and the respect that these males generally held for them had a pronounced effect on the behavior of individuals high in the dominance structure.

It is apparent that the hostility of these Aggressive Females toward adult males was linked to the fact that they had offspring. They avoided close association with males whenever possible, excitedly urging or driving the cubs away from the male. At such times they became highly excited and alert. They paced around rapidly, looking from side to side, and breathing and puffing heavily. At no time, however, did one of these females hesitate to attack a male that could not be avoided. The number of actual fights observed between Aggressive Females and adult males and the individuals involved is presented in Table XIV. They were particularly hostile toward the Dominant Male, Number 12. This, plus the fact that Number 12 refused to retreat from these females explains the greater number of fights with this one individual. It also explains the lesser number of bluffs, or threatening behavior of the females toward Number 12. Lesser males were more easily discouraged by threatening behavior from females.

In Table XIV neither combatant is listed as victor in either

TABLE XIV

BEHAVIOR OF AGGRESSIVE FEMALES TOWARD ADULT MALES, 1959-1961

Behavior	No. of Instances Observed	Individuals Involved	
		Males	Females
<b>Fightings:</b>			
With Dominant Male	14	No. 12	Nos. 7, 34, 39, 112, 120. Mothers
With Other Males	9	Nos. 14, 30, 33, 41, 73, XX, Cutlip, Scarface	of Nos. 53, 26, 29, 109.
<b>Threatening Behavior:</b>			
Toward Dominant Male	10	No. 12	"
Toward other males	19	Nos. 14, 30, 33, 41, 73, XX, 60, 69, Cutlip, Scarface	"

fighting or threatening behavior. Practically all fights and all bluffs attempted with Number 12 could be labeled physically unsuccessful. Yet these "unsuccessful" attempts appeared to make Number 12 somewhat more cautious when approaching the females having cubs; from this standpoint, it would appear that the fighting and bluffing was beneficial to the females. Fights and bluffs attempted with males subordinate to the dominant animal were much more successful, both physically and otherwise. Number XX, the Sub-Dominant Male in 1961, was an exception. The severity of the fights and their duration depended upon the individuals involved. They were usually quite short, for the most part one minute or less.

As previously stated, these females were particularly aggressive toward the Dominant Male and his immediate subordinates. There was, however, one other male, Number 41, a member of the Defensive Males class, that all Aggressive Females attacked viciously whenever he approached. He tried to avoid these encounters, but several times as many as four females would attack him simultaneously. On July 13, 1960, he was attacked by Number 65 and the mother of 53. He fled, whirling a number of times to fight off the attacking females. They pursued him for approximately 1/4 mile before quitting the chase and returning to their cubs. Number 41 was chased a number of times, but this was the only instance observed where the females were so persistent in their attack.

This intense hostility toward the adult males obviously stems from the females' concern for their offspring. Aggressive Females were constantly checking their cubs while in the concentration area. There is a widespread belief among Park Service personnel that the cubs are eaten by adult males. This has never been witnessed, and nothing in my experience indicates that this occurs. Its possibility, however, is not ruled out. Cannibalism in black bears was verified by Wes Woodgerd and me in 1959 and by John Craighead in 1960 in Yellowstone. Troyer (1962 B) reports that Alaskan brown bear males have been observed to kill and eat cubs of the species on Kodiak Island. It is possible that the same is true of grizzlies.

### Defensive Adult Females

This class was made up of generally younger appearing females with cubs of the year and females with yearlings. They reacted to the adult males in much the same manner as the Aggressive Females except they were not so eager to fight. They would excitedly warn their offspring away from the male, and if this failed, often would threaten the male by rushing at him and by issuing vocal sounds. Very rarely, however, did one of these females actually fight a male.

In general, these females were not so watchful over their young. One might feed for as long as 10 to 15 minutes with no apparent concern for her cubs. The females with yearlings tended to let them fend for themselves more than when they were cubs. Some individuals, however, were relatively watchful. Females who were classified as aggressive the previous year still displayed some of their characteristic hostility toward adult males, but to a much lesser degree.

### Cautious Adult Females

This class includes all adult females with no offspring. The behavior of these females was different from Aggressive and Defensive Females in that little or no dominance was directed upward in the order against superior adult males. Females with offspring, particularly Aggressive Females, exerted a noticeable influence on the dominance behavior of superior males by constantly challenging them. This led to more actual fighting, at least when the Dominant Male was involved. Females with no offspring, however, paid little heed to adult males



except those in the Aggressive class and these were avoided at all times. Defensive Males were respected when clashes occurred, but most smaller males were relatively ignored.

Dominance behavior, as such, of these females was directed toward individuals of either sex on a level with and below them in the hierarchy. While the phase of the reproductive cycle governs the attitude of females toward superior male individuals, aggressiveness, size, and to some degree age, appear to be the determining factors in the social rank of females with no offspring. Those females displaying aggressiveness asserted their superiority over lesser individuals much more forcefully than did females tending to be more timid. Reaction to the Aggressive Males, however, was basically the same throughout the class.

#### Younger Age Classes

Sex did not appear to be a factor in the social status of younger bears and both males and females are included in these classes. Age appeared to be responsible for social rank in relation to all other bears, while size seemed to dictate the individual's status within the class. In general, dominance was not actively sought within the class but was exercised against weaker and less aggressive individuals during the course of normal activity.

Behavior of Young Adults, which includes those bears considered three and four years old, varied somewhat. While aggressive activity toward individuals higher in the social structure was generally of a submissive nature, there were those who displayed superiority toward

others within the class and lower in the dominance structure. There was, however, no "order of dominance" within the class.

Two-year olds exhibited behavior similar to that of the Young Adults. An exception were those two-year olds running with litter mates. These family groups were fairly close-knit and the members often displayed much more aggressiveness toward others than was true of lone individuals. They would "back up" one another and often threaten much larger bears. These bluffs were sometimes successful and the other bear would retreat; if bluffing was not successful, the two-year olds invariably retreated. No instance was recorded, in the three years, of litter mates attacking or, as a group, fighting a superior individual.

Weaned yearlings held a position low in the hierarchy. Yearlings still with their mother possessed her social rank and their attitude toward others imitated that of the mother, i.e., the family group functioned somewhat as an individual in the dominance structure. The young strengthened the position of the female, generally backing her up in any encounter. The behavior of weaned yearlings, however, was entirely different. They did not have the protection the female afforded and were quite timid and apprehensive of all other bears.

The effect the female had on the behavior of young individuals was clearly demonstrated in 1959 and 1960. Number 5 was apparently a weaned or orphaned yearling in the spring of 1959. A female, she was very shy and would run from even a cub of the year. Later in the season, she was "adopted" by a female with one cub. Number 5 soon appeared to gain confidence and became less wary. The female was not particularly

aggressive and was classed as a Defensive Female. In 1960, this same group, the cub now a yearling and Number 5 a two-year old, ran together and Number 5 was extremely pugnacious throughout the season, repeatedly challenging even superior individuals. The female was always close-by, however, when these bluffs were attempted. The "family" had broken up in 1961 but Number 5 still displayed much of her characteristic aggressiveness toward weaker or less aggressive bears.

Other similar examples of the female's effect on the behavior of offspring have been observed. Number 39, an Aggressive Female, weaned yearlings (Nos. 37 and 38) late in the spring of 1960. The yearlings, both males, were quite large and well developed and while still with the sow displayed her hostility and aggressiveness. After being weaned, however, they became shy and apprehensive of all others. The same was true of yearlings Nos. 43 and 52, cubs of Number 65 in 1960, and yearlings Nos. 53 and 114, cubs of an unmarked female in 1960. Both females were very aggressive and the cubs followed their example. After being weaned, the yearlings became shy and secretive.

This does not appear to be the case with bears weaned at two years of age. Apparently the extra year under the protection of the female, plus the greater rate of growth exhibited by these bears, establishes them more firmly in the social structure.

Orphaned cubs exhibited behavior quite similar to that of weaned yearlings. They were very wary and secretive and ran at the approach of another bear. Two cubs were known to be orphaned in 1959, six in 1960, and one in 1961. None of these cubs were marked except the one in 1961.

Observations were obtained on the two litter mates orphaned in 1959 and the single cub in 1961. The two cubs remained to themselves, avoiding all other bears throughout the season. It is believed that one of these cubs has survived through 1961. Its behavior has changed but little since 1959.

Number 78, the cub orphaned in 1961, was observed throughout the 1961 season. On June 22, two days after being orphaned, this cub apparently attempted to attach itself to a family group--Female Number 120 and her two cubs. Number 78 sighted the family group from a distance and ran directly to them. The female rushed forward and knocked the cub over an embankment. An approaching family group apparently frightened the female and she ran with her cubs, the orphan following closely. The female suddenly turned and struck the cub, knocking it down. It kept its distance thereafter, but remained within sight of the family. The following day it was observed alone, and for the remainder of the season it remained solitary.

It is believed that four of the eight cubs orphaned in 1959 and 1960 survived the first year of life and that one survived for two years. It is questionable, however, whether these cubs could survive to adulthood--they were quite small and in relatively poor condition. Their chances of survival to adulthood are considered less than those retained by the female.

#### Significance of Social Structure

Scott (1958) states that a population may be made up of many

subgroups organized on the social level. He further states, "A primary characteristic of a population is its numbers, which depend upon the reproduction and survival of its members. Each of these in turn is strongly related to the adaptive behavior of the species involved." The grizzly bear population in Yellowstone, while made up of definite subgroups, exhibits a low degree of social organization. Therefore the behavior of individuals and cohesive family groups, although falling within definite dominance classes, is oriented toward individual survival.

It is believed that the development of this social structure, manifested in the dominance classes, has been brought about by the environmental conditions existing in Yellowstone. The ability to form such a structure, however, is considered inherent in grizzly populations, rather than through adaptive changes in behavior. Large concentrations of grizzly bears occurred in historic times, and it seems reasonable to assume that similar social structures existed in these populations.

A dominance hierarchy functions to reduce the amount of actual fighting among members of a population (Tinbergen, 1953). This is directly related to survival. Most of the observations on assertion of dominance in the grizzly population were made where competition for food was involved and, in the case of adult males, during the breeding season. The assertion of dominance, however, was not limited to these instances. The aggressive, domineering individuals were more successful in obtaining food, whether at the concentration sites or in other

areas of the Park. In times of food scarcity, it would appear that natural selection would favor these individuals.

In general, the males displaying aggressiveness were more successful in the competition for breeding females. However, the males near the top of the dominance structure did not dominate the breeding activity. The degree of sexual excitation of a particular male, regardless of the dominance class to which he belonged, appeared to be the major factor governing that male's reproductive activity and the vigor with which he sought females in estrus. This degree of sexual stimulation varied with individuals in each dominance class; some Cautious Males were more active in the reproductive effort than were superior individuals, including the Dominant Male. Among the adult males exhibiting sexual excitation, the males high in the order, and particularly the Dominant Male, appeared to be stimulated more toward fighting than were those males lower in the structure. Consequently, superior males often abandoned a female while fighting or chasing an adversary and in his absence the female would accept the lesser males. It is possible that in this manner the dominance structure functions to assure fertilization of all females in estrus.

## REPRODUCTIVE BEHAVIOR

### Observations

Observations on reproductive behavior were confined to the Trout Creek segment of the population in all three years. Two hundred twenty-six observations on this type of behavior were recorded; 115 involved adult males and 111 were made on females in breeding condition. Actual copulation was observed 41 times and activity between males and females other than copulation, 55 times. Copulation was effected by the male mounting the female and clutching around her body with his forelegs. Duration of copulation ranged from 5 minutes to 41 minutes, the average being about 16 to 20 minutes. The bulk of the observations were made at the concentration site, but some breeding activity was noted in other areas of Hayden Valley.

### Number of Individuals Breeding

The number of individuals, both females and males, observed breeding in all three years are presented in Table XV. Seventeen females, positively identified as different individuals, were observed breeding. In addition, six were observed mating some distance from the observer and where poor light conditions made positive identification impossible. Twenty-seven positively identified males were involved in breeding activity during the three years. In addition, six were observed under circumstances where identification could not be

TABLE XV

NUMBER OF DIFFERENT INDIVIDUALS OBSERVED BREEDING, 1959-1961

	<u>No. Different Bears</u>				<u>No. Diff. Days</u>		<u>No. Diff. Days</u>		<u>No. Diff. Times</u>		<u>No. Diff. Times</u>		<u>Ratio, Breeding Females/ Breeding Males*</u>
	<u>No. Identified</u>	<u>No. Unidentified</u>	<u>No. Identified</u>	<u>No. Unidentified</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	<u>Bears Observed Breeding</u>	
	<u>Fem.</u>	<u>Males</u>	<u>Fem.</u>	<u>Males</u>	<u>Fem.</u>	<u>Males</u>	<u>Fem.</u>	<u>Males</u>	<u>Fem.</u>	<u>Males</u>	<u>Fem.</u>	<u>Males</u>	
1959	3	4	-	-	3	3	-	-	4	4	-	-	1:1.33
1960	5	10	1	3	10	10	1	1	12	12	1	1	1:2.00
1961	9	13	5	3	13	13	5	5	19	19	5	5	1:1.44
Total	17	27	6	6	26	26	6	6	35	35	6	6	1:1.59

\* Includes only identified females.



made. It should be pointed out that in each year the 17 females were different individuals, but the males were not. Two of the 27 males bred females in all three years and five bred females in two of the three years.

Table XV shows that the 17 different, positively identified females bred one or more times on 26 different days. They were bred by 27 different males (22 if males breeding in more than one year are considered) a total of 35 times. Some females were bred by as many as four different males on a given date and each was considered a separate mating. When a female was bred by the same male more than once on a given date, a single mating was recorded. The same male was observed to copulate with one female as many as six times in a single evening; only one mating was recorded in these instances, even though more than one mating appeared successful. This was done in order to simplify presentation of the data.

Table XV also shows that the ratio of identified breeding females to breeding males was 1:1.59 for the three-year period.

The frequency of breeding of the 17 identified females and the number of different males accepted by females breeding more than once are presented in Table XVI. Nine of the 17 females were observed to mate a single time; eight were observed mating 26 times with 18 different males.

A single mating was recorded for each of the six unidentified females. Three of these females mated with identifiable males and three with unidentifiable individuals.

TABLE XVI

FREQUENCY OF BREEDING OF 17 IDENTIFIED FEMALES, 1959-1961

	No. of Identified Females Observed Breeding a Single Time	No. of Identified Females Observed Breeding More Than One Time	No. of Times Observed Breeding	No. of Different Males Accepted
1959	2	1	2	2
1960	3	2	9	8
1961	4	5	15	8
Totals	9	8	26	18

Breeding Season

The breeding season extended from about June 10 to July 10. For all three years, the first observed mating occurred on June 9, in 1961, and the last on July 10, in both 1960 and 1961. Some activity may occur earlier in June--observations are lacking for this period. Breeding activity reached its highest intensity in late June. Table XVII shows that, for 17 individual females breeding one or more times on 26 different days, 13 or 50 per cent of the matings occurred during the period from June 21 to June 30. During the nine-day periods immediately preceding and following the June 21-30 period, six or 23 per cent of the matings occurred in each. These periods of observed breeding activity of identified females are graphically represented in Figure 4. One of the six unidentified females bred during the June 11-20 period, three during June 21-30, and two during July 1-10.

TABLE XVII

PERIODS OF OBSERVED BREEDING ACTIVITY IN 17 IDENTIFIED  
AND 6 UNIDENTIFIED FEMALES, 1959-1961

Period	No. of Identified Females Observed Breeding	Per cent of Total Identified Females Observed Breeding	No. of Unidentified Females Observed Breeding	Per cent of Total Uniden. Females Observed Breeding
June 1-10	1	4	-	-
June 11-20	6	23	1	17
June 21-30	13	50	3	50
July 1-10	6	23	2	33
Totals	26	100	6	100

Estrus Periods

Considering the population as a whole, the number of females observed in estrus followed a curve suggested by Figure 4--50 per cent of the observed matings occurred in late June. There appeared to be some variation, however, in the length of the estrus period in individual females. Some were observed to breed a number of times over a rather extended period while others bred but a single time. It is realized that not all the breeding activity was observed; however, behavior of individual females and interest shown them by males at the concentration site appeared to indicate a particular female's breeding condition. Females in estrus attracted, and were receptive to, practically all adult males. Prior to the estrus period, females attracted

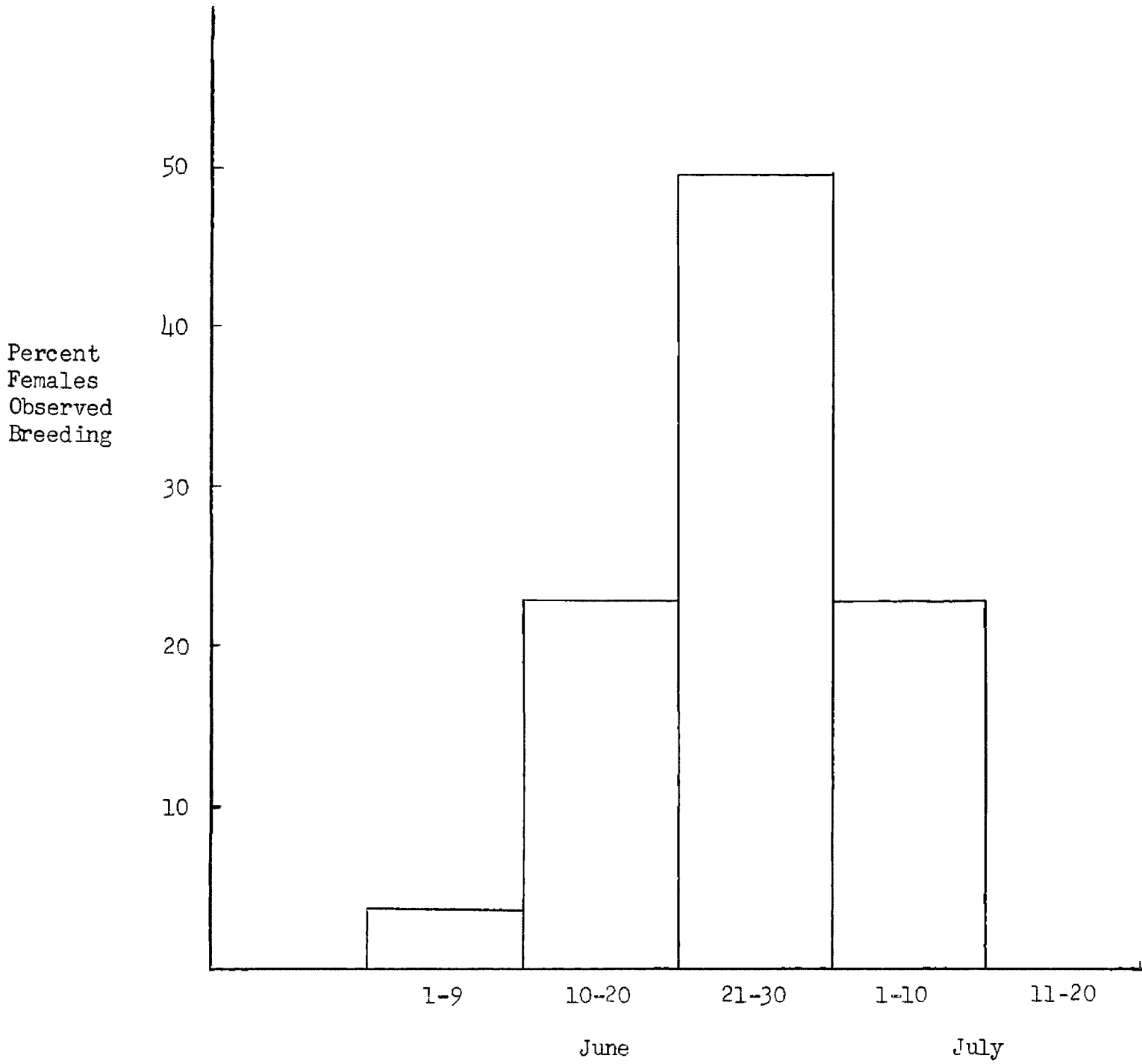


Figure 4. Period 26 females observed breeding, 1959-1961.

fewer males and were receptive to none of them. After estrus, they were ignored by the males.

Observations on three females before, during, and after estrus are presented in Table XVIII. The estrus periods of these three females typify fairly closely that observed in all identified females. Number 65 exhibited reproductive behavior on June 9, 10, and 11 in 1961. Several males displayed interest in her, but she was not receptive to any of them. She was not observed on June 12, 13, or 14, but was observed breeding on June 15. From June 16 to June 21, she displayed reproductive behavior but accepted none of the males that were attracted to her. No observations were obtained for June 22, 23, and 24, but on June 25 and 26 this female bred again. The following day, June 27, and for the rest of the season, she exhibited no reproductive behavior and no males displayed interest in her.

Number 15, a young appearing female, was first observed on June 21 in 1961. She was not observed again until June 26. This female showed no reproductive behavior on either date and no males were attracted to her. On June 28 she attracted a number of males and was receptive to their advances. She was bred by one large male while the observer was present. On June 30, this female displayed no reproductive behavior and was ignored by all males. This remained unchanged until the end of the observational period.

Number 12's Mate was a large female that Number 12, the Dominant Male, attempted to defend in 1960. She was first observed with the Dominant Male on June 17, and again on June 24, 25, and 26. She

TABLE XVIII

OBSERVATIONS RELATED TO ESTRUS PERIODS IN THREE FEMALES

Female	Behavior Prior to Breeding	Actual Breeding	Behavior After Breeding	Duration of Observations, in Days
No. 65	June 9	June 15	June 16	27
	10	25	17	
	11	26	18	
			19	
			20	
			21	
			27	
			28	
			30	
No. 15	June 21	June 28	June 30	21
	26		July 2	
			3	
			6	
			9	
			11	
		12		
No. 12's Mate	June 17	June 30	July 2	31
	24	July 1	4	
	25	3	5	
	26	6	13	
		10	14	
			17	
			18	

definitely exhibited reproductive behavior on each of these dates, but accepted no male. No observations were made from June 26 through June 29. On June 30 and July 1 she was bred by four different males. She attracted a number of males on July 2, but all were driven off by Number 12. July 3 she bred again, but on July 4 and 5, the Dominant Male drove away other males. This female bred again on July 6 and 10,

mating with the Dominant Male on the latter date. When again observed on July 13 and thereafter, she displayed no reproductive behavior. The Dominant Male and all other males exhibited no interest in her for the remainder of the season.

## SPECIFIC REPRODUCTIVE BEHAVIOR

### Adult Males

Dominance was most vigorously asserted by adult males during the breeding season. Sexually stimulated males were more aggressive than they were at any other time. The Dominant Male, Number 12, and the Sub-Dominant animal in 1961, Number XX, were extremely pugnacious toward all other individuals during this period--females exhibiting reproductive behavior were the only exceptions. Aggressive Males' behavior toward others was not so pronounced, but, in general, showed more aggressiveness than at other times of the year. The behavior of Defensive and Cautious Males toward individuals lower in the social structure varied from those that were more aggressive to those that remained about the same throughout the season.

Sexually aroused males were easily recognized, even at some distance. Some variation in behavior existed, but generally they exhibited a characteristic stiff-legged, swaggering walk. When approaching another bear this walk was exaggerated, the neck was bowed and the head was held low. They salivated profusely and frequently urinated on the belly and hind legs. Others appeared to recognize this behavior and hastily avoided males in this condition. Females in estrus allowed these males to approach, but often cowered before them.

Dominant Male. The Dominant Male, in all three years, displayed



excessive aggressiveness toward all others during the breeding season, particularly toward males high in the dominance order. He actively defended a single female each year, and in 1959 and 1960, relatively ignored other females in estrus. Late in the season in 1961 after quitting the female he had defended, he did display sexual interest in two other females but was not observed breeding with them. This male was observed mating only with the female he was observed to defend in each of the three years; the female, however, was receptive to a number of other males. He was observed breeding only one time in both 1959 and 1960, and on two different occasions, both with the same female, in 1961.

Number 12's intolerance of all others during the breeding season, with the exception of his "mate," was observed in all three years. This male and Number XX were the only males that attempted to defend a certain female. In situations such as this when the same male and female associated for a period of time, they are referred to as being "mates." The Dominant Male defended a single female throughout the breeding season in 1959 and 1960 and until June 26 in 1961. He attempted to keep all bears, regardless of sex, age, or size away from this female. The pair usually appeared together at the concentration site, and Number 12 would immediately race about, chasing all bears from the area. He would then return to the female and nuzzle and make overtures to her while she fed. Rarely did he feed, but remained watchful and chased others when they approached too closely.

This male was exceedingly hostile toward males immediately

subordinate to him in the dominance structure. When one of these males entered the area, Number 12 invariably rushed to attack him, and then often chased him for 1/4 mile or more. A number of times when this occurred, the female would also leave and usually other males were attracted to her. Upon returning, the Dominant Male would search about, uttering roars and groans until, apparently finding the female's scent, he would start off in the direction she had gone. He never failed to locate the female and drive away the other males.

In 1959 and 1960, the Dominant Male exhibited interest in no female other than the one defended by him. After mating with each of these females, on July 6 in 1959 and July 10 in 1960, he no longer defended them and displayed no further reproductive behavior. His aggressiveness toward individuals lower in the social structure also changed --they were tolerated much more than before. In 1961 his behavior was essentially the same--he defended a single female and was last observed breeding her on June 26. After that date he retained his aggressiveness toward others and was observed showing interest in two different females, but was not observed breeding either of them. One of these was the female defended by Number XX. Only July 9, Number XX and his "mate" appeared together at the concentration site. Number 12 drove Number XX away, then turned his attention to the female. She was not receptive to him, however. Number XX returned a short time later and made straight for the Dominant Male. A short but furious fight ensued and Number 12 was the victor. He did not pursue the other and Number XX reclaimed the female; later, the same day, the two were observed

breeding.

Sub-Dominant Male. This male, Number XX, was sufficiently aggressive in 1961 to warrant classification above other Aggressive Males. The relationship of this male to the dominant animal has been discussed under Dominance Behavior.

Number XX was present in 1960 as a recognizable individual and was classed as an Aggressive Male. He displayed aggressiveness characteristics of this class. During the breeding season, he exhibited interest in several females, and was observed breeding two different individuals.

In 1961, Number XX was much more aggressive than in the previous year. He attempted to defend one female and was successful in driving away all males except Number 12. His behavior toward individuals lower in the dominance structure paralleled that of the Dominant Male--no bear was allowed to come near the female. Unlike the Dominant Male, however, he often left this female and made advances to other females in estrus. He was observed mating with three other females, as well as the one he defended, in 1961.

Other Adult Males. The reproductive behavior of adult males other than the Dominant and Sub-Dominant (in 1961) males varied in different individuals. These males represented the three other dominance classes of adult males--the Aggressive, Defensive, and Cautious classes. None of these males appeared to defend a particular female, although some appeared to be mated with a single female for a period

of several days. The pair would arrive at the concentration site together and often leave together, but the male made no attempt to defend the female against others. The degree of sexual stimulation appeared to be somewhat different in each male. Some actively sought females in estrus and vied with more dominant individuals for these females; others appeared to breed only when the opportunity presented itself and when more aggressive males were not in the vicinity. The dominance class in which an individual was classified had no apparent effect on the degree of sexual stimulation and the vigor with which that individual sought females in breeding condition; some Cautious Males were more active than some belonging to the Aggressive and Defensive classes. Table XIX shows that adult males in all dominance classes played an active part in the reproductive effort. The larger number of breeding males in the Cautious and Defensive classes is due to the fact that more males comprised these two classes (Figure 3).

TABLE XIX

DOMINANCE CLASS OF 27 IDENTIFIED MALES OBSERVED BREEDING  
ONE OR MORE TIMES, 1959-1961

Year	Dominant Class	Sub-Dominant Class	Aggressive Class	Defensive Class	Cautious Class
1959	1	-	2	-	1
1960	1	-	3	3	3
1961	1	1	1	4	6
Totals	3	1	6	7	10

### Breeding Females

The reproductive behavior of females varied somewhat but in many respects was more stereotyped than that of the males. They played a much more passive role in reproductive activity than did the males. The length of the estrus period appeared to differ with individuals, as did the number of times a female bred and the number of different males that were accepted. These variations were pointed out in Tables XVI and XVIII. Behavior that appeared to be fairly uniform included reaction to sexually aroused males before and during the period of estrus, and behavior after the breeding period. The degree of an individual female's aggressiveness, as exhibited at other seasons of the year, did not affect her reproductive behavior--all females displayed essentially the same basic behavior.

Practically all females demonstrated some reproductive behavior a number of days before they were observed breeding. Different males were attracted to them and displayed varying degrees of sexual excitation. Some males were permitted to approach closely and to smell the genital region, but none of these males were allowed to actually mount the female and no mating was observed. Females actually in estrus were generally receptive to all males. At the approach of an aroused male, the female invariably cowered and assumed a submissive attitude. Some males mounted the female immediately; others nuzzled and made overtures for a time before attempting copulation. As previously stated, duration of copulation ranged from 5 minutes to 41 minutes, the average

being about 16-20 minutes. Females were observed to mate, some apparently at random, with adult males of all dominance classes. The Dominant Male was an exception--some females in estrus, other than the one defended by him, attempted to avoid this male.

The breeding period ended abruptly for all females. Females observed attracting a number of males and breeding on one evening were relatively ignored by all males the following day. For the remainder of the season their relationship to adult males assumed that which was described under Dominance Behavior.

#### Male-Female Relationships

The Dominant Male's relationship with a single female was somewhat different from that of other individuals. This relationship was basically the same in each of the three years. The pair invariably arrived at the concentration site together and remained together, except for the times when Number 12 was fighting or chasing others. On these occasions the female was receptive to other males. The pair was observed a number of times lying together for more than an hour, wrestling and rolling at times. Number 12 often nuzzled the female and mouthed and bit at her ears and neck. He made no attempt to breed the female on these occasions until late in the season in 1959 and 1960. After breeding in each of these years, he quit the female altogether. In 1961, he was observed breeding the female on June 15 and again on June 26, after which he displayed no further interest in her.

Other males and females were observed to show this behavior

toward each other but for a relatively short time and usually during the female's estrus period. Different males were also often involved with the same female. Murie (1944) describes similar mating behavior in grizzlies in Alaska.

Specific Breeding Activity. Breeding activity observed on some occasions is worthy of mention.

On June 26, 1959, one of the two old males vying for the position of dominance was observed breeding a large, dark colored female. Some time later, the other old male approached the breeding pair and drove off the male. He then mounted the female and began copulation. The displaced male wandered away a short distance and lay down. After 10-12 minutes he suddenly got up and rapidly approached the pair. The breeding male dismounted as the other approached and turned to meet him. They did not fight but made false lunges at each other until the second male turned and walked away. The first male then reclaimed the female and once again mounted and copulated with her for 14 minutes. This illustrated the equality of dominance of these two old males early in 1959. It was also the first observed promiscuity of a female, which later was observed many times.

Two females in estrus, Numbers 7 and 39, were present at Trout Creek on June 12, 1961. Six adult males, including the Dominant and Sub-Dominant animals were also present and all vied vigorously for the females. In a period of about two hours, female Number 7 copulated ten times with four different males. Female Number 39 was mounted eight times by two different males. The Dominant Male was the only

male observed not to breed--he spent the entire period exercising his dominance over the other males, chasing first one from a female and then returning and pursuing another. Displacement of breeding males was also exercised by some of the other males. Neither of the two females were observed until several days later--Number 7 on June 19 and Number 39 on June 17. On these dates they attracted no males and their breeding period had apparently ended.

The Sub-Dominant Male, Number XX, appeared on July 4, 1961, with the female he attempted to defend that season. The female was apparently in estrus and attracted several males, but was receptive to only one, a rather small male. Number XX was continually occupied with chasing away the other males. During the course of the evening, the small male mounted and began copulation with the female seven different times, but each time was chased away by Number XX. Late in the evening, Number XX and the female left the area together and bred approximately 1/4 mile from the feeding site.

#### Significance of Breeding Behavior

The similarity of the breeding behavior of the grizzly population in Yellowstone to that of historic populations or of other populations today is not known with certainty. As previously stated, concentrations of grizzlies did occur at this time of the year in historic times. Storer and Tevis (1955) make no mention of breeding activity in California, but Lewis and Clark reported that copulation occurred in June in what is now Montana (DeVoto, 1953). Specific relationships



of breeding bears in these concentrations, however, was not observed and may only be assumed.

Limited data are available on the reproductive activity of the grizzly. Murie (1944) observed breeding of a single female in Mt. McKinley National Park. This female was shared by two males for a period of about three weeks. The larger of the two males often chased the other from the female. One of the males was observed mating with the female on May 20 and June 2; the other bred the female on June 10. This was similar to behavior observed in Yellowstone. Seton (1909), reporting on grizzlies in zoos, states that breeding occurred in June and July and that one pair mated "many times."

The present situation in Yellowstone is believed to somewhat parallel that of large populations of grizzlies in historic times. Bears may roam unmolested over vast areas and make seasonal migrations to available food supplies. The inherent trait of grizzlies to congregate where food is easily obtainable, while perhaps intensified in the Park, is not considered unlike that described in the literature. It is possible that the breeding behavior occurring under these conditions has remained unchanged, and that reproductive activity witnessed in Yellowstone approximates that which occurred in concentrations of grizzlies in historic times. It also seems reasonable to assume that this pattern of behavior, somewhat modified, may exist in other relatively large localized populations today.

## SUMMARY

1. The study, one phase of a long-term ecological study of the grizzly bear, was conducted in Yellowstone National Park. For about three months during the summer, grizzlies concentrate at four major refuse dumps--Trout Creek, Rabbit Creek, West Yellowstone, and Gardiner--and afford opportunity for intensive observations. Behavioral studies were confined to the Trout Creek segment of the total population.

2. The habit of concentrating where food is available is inherent in grizzly bears and this behavior in Yellowstone somewhat parallels that of populations in historic times and in Alaska today. Supplemental food has affected dispersion and movement, but is not believed to be a major factor in determining population numbers. It is recognized that a constant food supply over an extended period of time may have altered some behavioral traits.

3. One hundred twenty-two grizzlies were individually marked over a three-year period. In addition, a number of unmarked but recognizable individuals and family groups were present. A three-year total of 1,809 observations was made on 179 different individuals and family groups.

4. Censuses were conducted by making direct counts at the concentration sites and in other areas of the Park. A minimum population figure of 154, 169, and 166 was arrived at in 1959, 1960, and

1961, respectively. The Schnabel Method of computing total population corresponded closely to the direct counts, but the figure obtained by use of the Petersen Index was significantly less.

5. Bears were classified in five age classes: cubs of the year, yearlings, two-year olds, young adults, and adults. The per cent composition of each of these classes remained relatively stable for the three-year period. Some discrepancy was noted in two-year olds, but may have been due to error of the observer. Sex ratio, as determined by captured bears, was essentially 1:1.

6. The Trout Creek population exhibited definite stratifications of its members. Five dominance classes were recognized. These were, in descending order of dominance, the Dominant Class, Aggressive Class, Defensive Class, Cautious Class, and Subordinate Class. A sixth, the Sub-Dominant Class, was added in 1961. Dominance was asserted most actively by those individuals near the top of the dominance structure.

7. Criteria used to classify adult males included aggressiveness, size, age and in some cases a combination of all. Aggressiveness appeared to be the major factor. Aggressiveness and reproductive condition appeared to govern females' behavior toward adult males, while aggressiveness, age, and size determined their social rank in relation to other members of the population. Sex was not a factor in the social status of younger bears, and they were classified mainly by age and size.

8. Some variability in behavior of individuals within each dominance class was noted, and was most striking in some members of

the Subordinate Class. Behavior toward members of other classes, however, was basically the same.

9. The same male actively assumed the dominant position in all three years. Four other males vied for this position with varying degrees of aggressiveness. The Sub-Dominant Male in 1961 displayed aggressiveness similar to that of the dominant animal.

10. Females with offspring, particularly those with cubs of the year, exhibited excessive hostility toward adult males. The behavior of individual females toward adult males was somewhat different each year, depending upon the particular female's reproductive status.

11. Families, i.e., females with offspring and weaned two-year old litter-mates running together, functioned somewhat as an individual in the social structure. Young bears still with the female appeared to be influenced by the behavior of their mother--aggressive females usually had aggressive offspring. Offspring weaned at two years of age retained this behavior but those weaned as yearlings became timid and apprehensive of others. Two-year olds running with litter-mates showed more aggressiveness toward others than did lone individuals of the same age.

12. Seventeen different, identified females and six unidentified females were observed breeding in the three-year period. Twenty-seven identified and six unidentified males were observed to breed. The identified females were bred by 27 different males a total of 35 times --nine females bred a single time and eight bred 26 times with 18 different males. The six unidentified females mated a single time.

13. The breeding season extended from about June 10 to July 10. The first observed mating occurred on June 9 and the last on July 10. Breeding activity reached its highest intensity in late June. Fifty per cent of the observed matings occurred during the period from June 21 to June 30 and 23 per cent in each of the nine-day periods immediately preceding and following June 21-30.

14. There appeared to be some variation in the length of the estrus period in individual females. Some were observed to breed a number of times over a rather extended period while others were observed breeding but a single time. Females in estrus attracted, and were receptive to, practically all adult males. Prior to the estrus period, they attracted fewer males and accepted none; after estrus, they were relatively ignored by the males.

15. Sexually stimulated males were more aggressive than at other seasons of the year and dominance was most vigorously asserted during the breeding season. Males high in the order were extremely intolerant of all others, except females in breeding condition. Females in estrus usually cowered and assumed a submissive attitude at the approach of an aroused male belonging to one of the higher dominance classes.

16. The Dominant Male, in each of the three years, and the Sub-Dominant Male in 1961, attempted to defend a single female. No other males exhibited this behavior.

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