

De Voto Bernard. 1953. The Journals of Lewis and Clark. Houghton Mifflin Co., Boston. 504 pp.

We have experiences that even ^{unmuffled} quiet activity close to a den ^{has} awaked ~~a~~ sleeping bears and jolting ^{them} with a hypodermic needle has invariably caused them to ~~start~~ ^{exit from} by ~~leaving~~ the den.

This divergence from ~~passing~~ the ^{construction} ~~use~~ of rough bedding ^{during} may indicate a tendency for pregnant females to select fine, soft materials for their winter beds.

The carcass of ^{one} ~~an~~ old bear found in spring suggested debility and death ^{resulting} from natural causes associated with old age.

p. 37- add Shoshone
change caption under Fig. 7

p. ? check p. 1 1967 ref.

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			<u>22</u>

Figure Legends

1. A Yellowstone grizzly bear, no. 65, with four cubs. An average of 33 cubs was produced annually by the Yellowstone population of between 175-200 animals. Population figures are based on 324 censuses ~~totalling 11,34~~ ^{in part} and calculations using observations of marked and unmarked bears.
2. Instrumenting a grizzly ~~in~~ with a ^{transmitter} ~~radio~~ collar in late fall. The collar which was slipped on over the bear's head and ~~was~~ ^{was} usually removed by the ~~bear~~ ^{grizzly} ~~soon~~ after emerging from a winter den.
3. Radio location system. Emphasis was placed on a design providing flexibility for field studies.
4. Transmitter collars and a portable, directional receiver. Transmitter weighs 1.8 oz., the ~~battery~~ ^{transmitter} pack .9 lb.
5. Den ^{of Grizzly No. 40} excavated at base of tree. Roots frequently determined the size of the entrance.
6. Nearly vertical entranceway with ~~den~~ ^{bed} chamber lying directly beneath the tree.
7. The first winter den of grizzly no. 202 consisted of an ~~partial~~ ^{incomplete} excavation under a horizontal log.
8. Female No. 40 prior to final movement to her den. Dens were located in 1964, 1965, 1966 and 1968.
9. Den entranceway excavated through obstructing roots which were chewed off by the bear. Photograph was taken from den chamber looking out.
10. Den lined with conifer boughs. When grizzlies emerged ^{from hibernation} some of the bears raked the bed material out of the ~~den~~ den.

11. Diagram of den with bed lower than entrance. Such dens were covered with five to ten feet of snow.
12. Den constructed so the bed lay slightly above the entrance. The functioned as a heat trap and helped to provide a ^{relatively} constant den temperature until deep snow sealed the den entrance.
13. ^{Diagram of a} Black Bear den - a natural cave with a bed 18" deep and 30" in diameter.
14. Denning area of gizzly no. 202 in the canyon of the Yellowstone River. Isolation provided by the canyon or by remote timbered areas was characteristic of all denning sites.
15. Entranceway to den of gizzly no. 164. Typical tailings of excavated soil and rocks in lower right-hand corner served as beds for bears prior to entering dens for the winter.
16. A den ^{whose roof} ~~protruded~~ caved in after use. This and other such dens were found in the proximity of a fresh den dug by gizzly no. 164.
17. Rough bed constructed on the snow in March several hundred feet from the winter den. Female no. 40 and her offspring used this bed for several weeks before leaving the den area.

WILDLIFE MONOGRAPHS

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7 February 1972

Dr. Frank C. Craighead, Jr.
Environmental Research Institute
P. O. Box 156
Moose, Wyoming 83102

Dear Frank:

Thank you for your letter of 2 February with the sponsorship page for the grizzly bear Monograph. Even though it is a little bit longer than usual I think it can be made up into a rather attractive sponsorship.

If I don't hear from Bill Osburn by the end of this week I will call him and find out why he hasn't returned the manuscript to me.

With very best wishes,

Cordially,



Louis A. Krumholz
Editor

March 7, 1972

Dr. Louis A. Krumholz
Department of Biology
University of Louisville
Louisville, Kentucky
40208

Dear Louis:

I have read over Jonkel and Cowen's monograph on the black bear and have made the following references to it:

On Page 27 of the grizzly manuscripts, the ninth line after the word "trees", I have inserted "Jonkel and Cowen, (1971) state that the base of a hollow tree was the site most often used for denning by black bears. These dens were within, not under, the trees". The reference to literature cited should read: "Jonkel, C. J. and Cowen, Ian McT., 1971, "The Black Bear in the Spruce-Fir Forest", Wildlife Monograph No. 27. 57 pages.

Since sending the manuscript to you, I have had an opportunity to do more editing. It might be well for me to make these changes before final page proof. Have you received the manuscript returned by Dr. Osburne, and if so, what were his comments, as well as those of the other reviewer?

I am planning to attend the North American Wildlife Conference in Mexico City and will look forward to discussing the manuscript with you at that time.

Sincerely,

Frank C. Craighead, Jr.

FCC,Jr.:mr

Item (10)

GRIZZLY BEAR PREHIBERNATION AND DENNING ACTIVITIES
AS DETERMINED BY RADIOTRACKING

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INTRODUCTION

Grizzly bears (Ursus arctos horribilis Ord) were seen and collected on our western prairies in 1805 by Lewis and Clark, who recognized them as a species distinct from the black bear (Ursus americanus Audubon and Bachman). Grizzlies have disappeared from most of the western states where they were once common. In just over two human life spans, the grizzly has become an endangered species in the contiguous 48 states. Storer and Tevis (1955) estimated that in California alone the original grizzly bear population was around 10,000 animals. The last grizzly in California was seen in 1924. In Yellowstone National Park and adjacent portions of four national forests, an area of approximately 5,000 square miles, there are between 175 and 200 grizzly bears (Craighead and Craighead 1967). This is probably the largest discrete population of grizzlies left in the Continental United States except for Alaska.

Because the Yellowstone grizzly is largely nocturnal, inhabits a heavily timbered area of rugged terrain and enters its den for a winter sleep that lasts 5 to 6 months, it was necessary to develop and employ a radiotracking and locating system (Craighead et al. 1963, Craighead and Craighead 1965). Such a system enabled us to gather data on den site selection, den construction, prehibernation behavior and denning activities as one facet of a comprehensive ecological study of the grizzly bear (Craighead et al. 1960).

Prior to this study, little was known concerning the denning activities and prehibernation behavior of wild grizzlies. Dens

reported to us, as those utilized by grizzlies, turned out to be the dens of black bears. It was generally thought that the Yellowstone grizzlies, like black bears and the European brown bears (Ursus arctos arctos L.), utilized natural shelters -- caves, hollow trees, windfall and dense vegetation -- as sites for their "hibernation" dens (Couturier 1954). These were supposedly enlarged by digging, or improved to varying degrees as shelters for the long winter sleep.

In November 1963, we successfully tracked a 5-1/2-year-old female grizzly, No. 164, to her winter den (Craighead and Craighead 1965). As far as we know, this is the first instance in which a radio transmitter was used to track and locate a grizzly bear as it entered its winter den.

In 1961 we began developing and testing radiotracking equipment and we continued this work through the fall of 1968. During this 8-year period, we made 48 instrumentations of 23 different grizzly bears. These animals were tracked or monitored for a total of over 1,200 tracking days; den location sometimes required monitoring for 3 months and intensive tracking for 4 consecutive days. Grizzly bear No. 40 (Fig. 1) was instrumented and monitored for portions of 8 consecutive years. Seven other bears were instrumented and monitored during 2 consecutive years each. The winter dens of six different grizzlies were located, but since more than one den was located for some bears over a period of years, we were able to obtain information on size and construction of 11 dens. Due to involvement of family groups,



Fig. 1. Female grizzly bear equipped with radio collar. This grizzly, No. 40, was radiotracked for portions of 8 consecutive years. Note placement of numbered ear tags and individualized color markers.

22 animals were radiotracked and observed to have utilized the 11 dens.

A short discussion of hibernation, or winter sleep, seems appropriate since differences in hibernators, and variances in how they hibernate, have caused researchers to formulate varying definitions of this phenomenon. Species differ in the duration of hibernation, the degree of drop in body temperature, the relation of body temperature to ambient air temperature, the accumulation of fat reserves, the depression of metabolic activities, and the variations in specialization of individual organs and tissues for functioning in the hibernating state. The bear, for example, shows less change in body functions and is generally considered less of a "true" hibernator than the ground squirrel (Lyman and Dawe 1960, Kayser 1961).

If we use Hock's (1960) definition of hibernation -- ". . . a periodic phenomenon in which body temperature falls to a low level, approximating ambient, and heart rate, metabolic rate, and other physiologic functions fall to correspondingly minimum levels . . ." -- the grizzly bear is not a hibernator. Instead of hibernation, Hock has proposed the term carnivorean lethargy to describe the bear's winter sleep. Hock also pointed out, as have others, that hibernators must compress their annual cycle of activities into a few months. Nearly all facets of hibernators' life histories and consequently their physiologic functions reflect the fact that they are constantly preparing for hibernation, hibernating, or recovering from the condition. Thus, the whole year is involved in a cyclic phenomenon that is related

to hibernation. In northern latitudes, this is true of bears.

Authors suggesting that the bear is not a hibernator point out that, though bears go into a deep sleep and are inactive for considerable periods of time, they do not become torpid and helpless, as do most hibernators (Kayser 1961:21-50). Bears can be readily aroused after which they can react quickly and energetically to disturbance, and their body temperature does not approach the ambient air temperature. The temperature of wintering female bears was found to be 84.2°F. to 93.2°F. (Kayser 1961). After anesthetizing and instrumenting a hibernating black bear, we recorded a depressed body temperature of 83.5°F. (due to drug action) which gradually rose to 96.7°F. over a period of 21.5 hours (Craighead and Craighead 1966). Temperatures taken every half hour over a 24-hour period ranged from 93.7°F. to 96.3°F. (Craighead and Craighead 1967). This is a drop in body temperature ranging from 4.7°F. to 7.3°F. below the body temperature of 101°F. recorded during summer. Folk (1967) obtained a low heart rate of 8 beats per minute from a hibernating grizzly in captivity and Kalabukhov gives the respiratory frequency for a wintering European brown bear of 12/min. (Kayser 1961). Hibernating bears show a marked depression in heart rate and respiratory frequency, but a relatively slight drop in body temperature.

In animals of all sizes, potential energy reserve is proportional to body weight. Also basal metabolic rate is weight dependent -- the larger the animal, the lower the metabolic rate. Larger animals

can thus fast longer than smaller ones without a modification in metabolic level. A bear with fat reserves going into winter sleep can fast 200 days (7 months) with only a slight reduction in body temperature. This is not possible for "true" hibernators. Morrison (1960) stated that because of its low thermal conductance, the bear cannot maintain a body temperature near the ambient air temperature. He concluded ". . . in any event, it is clear that bears lie in the interfacial zone between animals which might last through the winter at or near their basal metabolic rates and those which cannot." The limited depression of body temperature observed in bears may qualify them as "ecological" hibernators and disqualify them as "physiological" hibernators (Morrison op. cit.). This distinction is useful if we recognize that black and brown bears are superbly adapted to sleeping through long winters without great modification in metabolic level and in this sense are hibernators.

Hibernation is generally considered to be a torpid state in which the hibernator, partially or wholly, loses its sensibility or power of motion. This is a state from which the animal can be aroused only with difficulty. Thus, bears during their winter sleep are dormant rather than torpid because they can be rather easily aroused and they can move rapidly when disturbed -- features enhancing survival of a group of mammals that have been hunted by man since prehistoric times. Low ambient air temperatures, deep snow, and the unavailability of food appear to make hibernation or winter sleep essential to the survival

of grizzlies in the Yellowstone area.

ACKNOWLEDGEMENTS

This phase of a long-range, ecological study of the grizzly bear could not have been conducted without the help of numerous individuals and support from many organizations. We extend special thanks and credit to Joel Varney, who designed and constructed the radiotracking equipment; to Bart O'Gara for helpful suggestions; to Maurice Hornocker; Robert Ruff; Henry McCutchen; Charles Ridenour; Harry Reynolds, III; Harry Reynolds, Jr.; Jay Sumner; and Jack Seidensticker; all of whom, at one time or another, aided us in testing equipment, collaring animals, or tracking grizzly bears to dens or den sites. The comradeship developed during these times and the sharing of exciting and challenging experiences are not recorded in this paper but, nevertheless, they are very much a part of it.

Special thanks are also due Mr. Lemuel Garrison, former Superintendent, and other personnel, of Yellowstone National Park; Dr. Melvin M. Payne, President, National Geographic Society; and Mr. Frank H. Goodyear, Treasurer, Environmental Research Institute. All, in different ways, encouraged us in our research efforts.

This study was supported throughout its entirety by the National Geographic Society; it was also supported by Research Grant GB-2672 from the National Science Foundation; continuing Grant AT (45-1)-1929 from the Atomic Energy Commission; and funds from the

Bureau of Sport Fisheries and Wildlife.

In addition, we gratefully acknowledge financial aid from the Environmental Research Institute and the Philco-Ford Corporation. We received help and cooperation from the National Park Service, the University of Montana, the Montana Fish and Game Department, the State University of New York at Albany (Atmospheric Sciences Research Center), and the Yellowstone Park Company.

STUDY AREA

The study area in Yellowstone Park and the surrounding national forests lies largely between 7,000 and 8,000 feet altitude. Extremes are reached at Electric Peak (11,155 feet) and near Gardiner, Montana (5,282 feet).

Eighty to 85% of the area is timbered, and most of this lies within the spruce-fir (Picea-abies) zone. Lodgepole pine (Pinus contorta Dougl.), in transition to the spruce-fir climax, covers nearly 75% of the Park (Baggley and McDougall 1956). Sagebrush and grass dominate dry areas of rich soil for long periods before finally succumbing to the invasion of lodgepole pine and, in some instances, aspen (Populus tremuloides Michx.). Areas of sagebrush-grass are important to the grizzly bear. Other habitats important to grizzlies are the alpine and subalpine meadows of sedge-bluegrass (Carex-Poa). These are characterized by grasses, sedges, and numerous dwarf herbaceous plants. Such open-land types in combination with timbered areas appear

essential for optimum grizzly bear habitat. The open types provide the bulk of their food, and the timbered areas provide food (such as berries and pine nuts), daytime retreats, and denning sites. Although the timbered land consists primarily of the relatively sterile lodgepole pine forests, there are extensive areas where these are being invaded by limber pine (Pinus flexilis, James) and whitebark pine (Pinus albicaulis, Engelm.), both of which, when mature, furnish crops of pine nuts in favorable years. A variety of berries in burned-over areas and in the understory of timbered types are eaten by grizzlies. The most important are the big whortleberry (Vaccinium membranaceum Dougl.) and the grouse whortleberry (Vaccinium scoparium Leiberg).

The average maximum temperatures during the summer are in the seventies. The highest recorded temperature is 98°F., and the lowest -66°F. Temperatures of -40°F. and below have been recorded, at some time, from all areas of the Park where temperature records have been kept. Snowfall is heavy over most of the Park; annual snowfall averages close to 150 inches. Annual precipitation varies from 13.73 to 38.26 inches (Anon. 1959).

Carrion forms a considerable portion of the diet of the grizzly bear, and its availability and abundance influences grizzly bear activity and behavior, especially prior to and following hibernation. In Yellowstone National Park, the estimated populations of large mammals include: black bear, 500; pronghorn (Antilocapra americana Ord.), 170; bighorn sheep (Ovis canadensis Shaw), 600; bison (Bison bison L.).

580; mule deer (Odocoileus hemionus Rafinesque) in winter, 500; elk (Cervus canadensis Erxleben) in winter, 8,300; and moose (Alces alces Nelson) in summer, 450 (Anon. 1970).

Carnivores sufficiently numerous to compete with the grizzly for food include the coyote (Canis latrans Merriam), black bear, and badger (Taxidea taxus Shreber).

METHODS

To obtain information on prehibernation behavior and denning activities of grizzlies fitted with radio transmitters, the position and movements of instrumented bears were plotted from the intersection of bearings (fixes) which were made from a distance. Then, guided by the fixes and using portable directional receivers, we moved on foot to observe the animals at close range.

The radiotracking system was designed to be as flexible and portable as possible to provide maximum use in various types of field work. A block diagram of the location system is shown in Fig. 2. The transmitter collar radiates a pulsed signal which can be received by a variety of stations, depending on the desired range and portability of the receiver.

A small, 2 lb. battery-operated receiver with a directional loop antenna was used for tracking on foot when the distance between the receiver and the instrumented animal was not greater than 3 to 4 miles (Fig. 3). The range was limited by the small size of the antenna

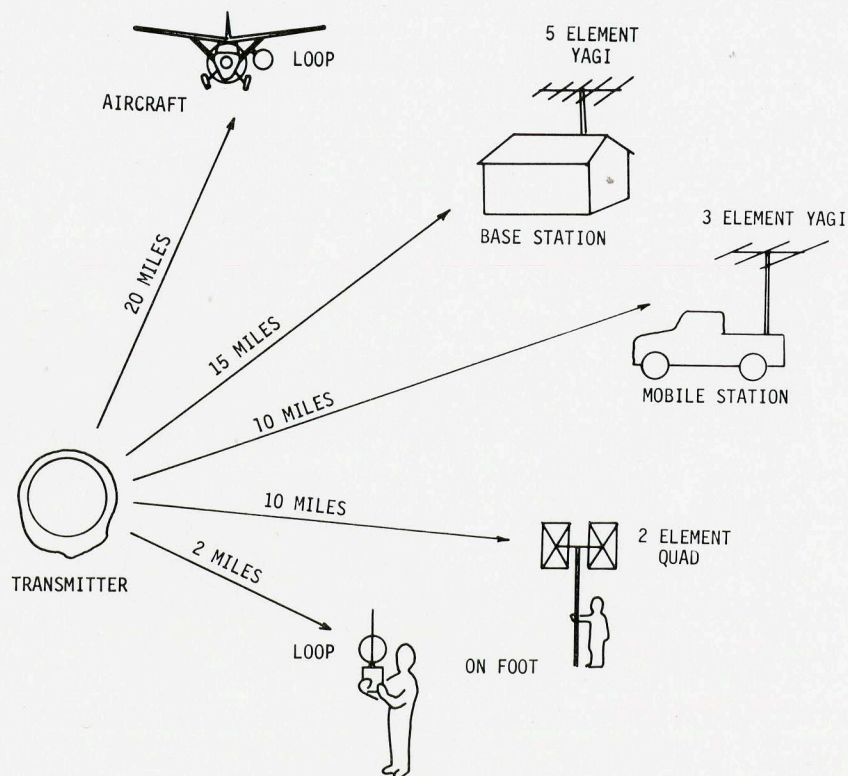


Fig. 2. Radio Location System

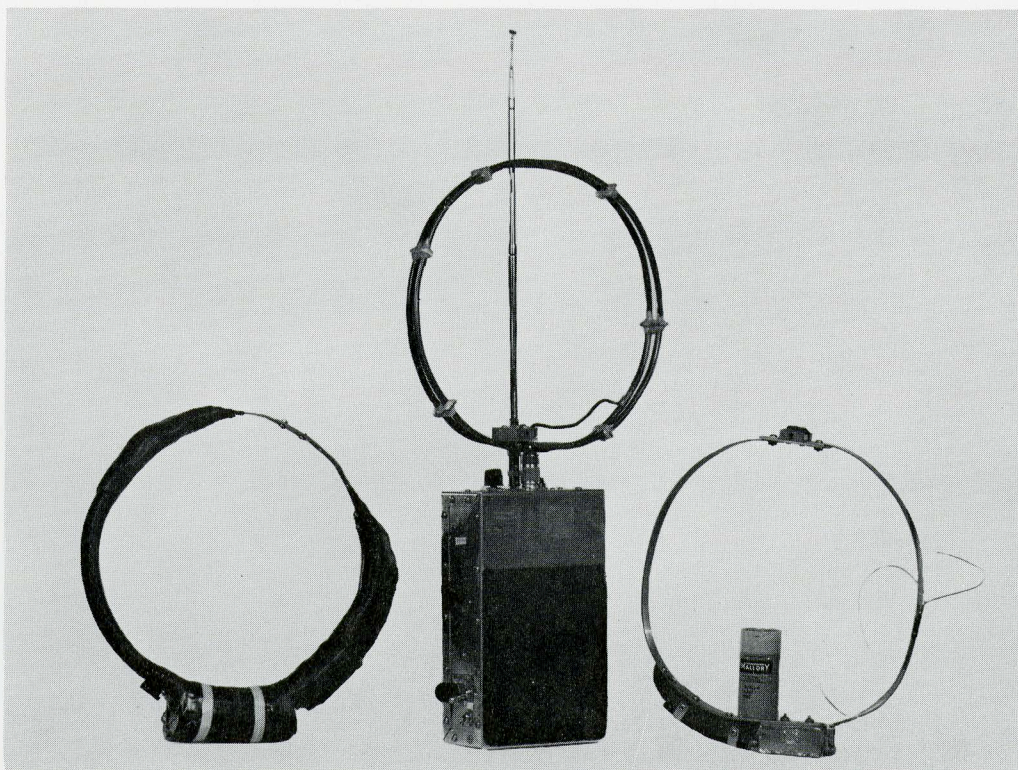


Fig. 3. Transmitter collars and a portable, directional receiver.

and varied greatly with shielding effects in mountainous terrain. For longer range, a larger quad antenna was used with the same receiver. When an animal was in a location where tracking from nearby roads was possible, a 3-element yagi antenna mounted on a vehicle provided an accurate working range up to 10 miles. A more sensitive, 5-element yagi antenna located at a base station gave a maximum range of 15 miles. Fixed-wing aircraft or helicopters with the directional loop antenna mounted on the fuselage were used for more remote locations with up to a 20 mile range. The transmitter collar which was placed on the animal to be tracked consisted of the transmitter unit and a battery pack attached to a circular metal strap which acted both as a loop antenna and a collar. The assembly was covered with fiberglass-reinforced acrylic resin to protect the electronics and batteries, and to prevent flexing and bending which would otherwise have caused antenna detuning or eventual breakage. The inside of the collar was padded with rubber hosing or foam rubber or a combination of both to make it fit the animal snugly and comfortably.

The collar was designed so the metal strap could be adjusted to the desired neck diameter by inserting two screws in a series of holes in the overlapping ends of the strap at the time it was placed on the animal. After the screws were placed and tightened, the collar tuning was adjusted for resonance with the aid of a field strength meter. Field measurements showed, however, that the shift in antenna tuning was negligible, if the strap length was not changed when the

collar was placed on the animal. Thus, we decided to tune the antenna in the laboratory. This was possible since the size of the animal's neck was known from previous measurements or it was possible to estimate this from our weight records while the collar was being prepared. This eliminated field tuning; final adjustments to collar size were made by adding or removing a small amount of padding when placing the transmitter on the animal.

Power for the transmitter was provided by a pack of seven Mallory*, type Rm-1450, low-temperature, mercury cells. The battery pack was waterproofed by a combination of electrical tape, wax, and silicone rubber. It was attached to the collar next to the housing of the transmitter. A photograph of two radio collars and a portable receiver is shown in Fig. 3.

We used two types of transmitters in tracking operations. One type was designed to operate continuously, emitting a 50 ms pulse at approximately 1 second intervals. The battery life with this type of transmitter (called the standard model) was 3 months. In some cases we required a longer lifetime, so an additional timer circuit was used to turn the transmitter on and off at 30 second intervals. This type of transmitter was called the extended life model. Battery life was 9 months. All transmitters of both types operated on the same frequency, but each had a different pulse rate which allowed each grizzly to be identified.

* Use of brand names does not imply endorsement of a product by the authors or the supporting agencies.

Transistorized receivers were used for tracking on foot and from base and mobile stations. Various kinds of antennas could be connected to a receiver, depending on the location in which it was used. The receivers were battery-operated, Citizen's Band units modified to operate at 32 MHz. Early in the study some tracking at base and mobile stations was done with general-coverage communications receivers; however, these were later discarded in favor of the portable units.

Summaries of the transmitter, receiver, and system characteristics are given in Tables 1, 2, and 3.

The accuracy of directional bearings depended on the type of antenna being used. The loop antenna provided the most accurate bearings of any of the antennas because its pattern has two sharp nulls which allow determination of the direction of a signal within a few degrees. Because of its small size, it was the least sensitive antenna, but it was more useful than other antennas at short range. The accuracy of directional bearings taken with the loop antenna was sometimes reduced by propagation effects in the mountainous terrain in which the tracking was conducted; dense timber could cause multiple reflections of the signal which obscured the null in the antenna pattern, and reflections from large topographic features such as hillsides and cliffs sometimes gave false bearings. Such problems could be circumvented when moving in on an animal by hiking to a slightly different location, climbing a tree, or continuing to move on in the general direction of the signal until conditions improved enough to permit more accurate bearings to be taken.

TABLE 1.--TRANSMITTER CHARACTERISTICS

Frequency	32 MHz
Output power	100 mW pulse
Pulse width	50 ms
Pulse repetition rate	1 per second (nominal)
Antenna type	resonant loop, 11 inch diameter
Antenna impedance	50 ohms
DC input power	280 mW peak, 18 mW average
Battery type	mercury, low temperature 9.3 volts, 4.5 Ah
Weight:	
electronics	0.1 lb
battery	0.9 lb
complete collar	2.0 lbs
Operating lifetime	3 months standard, 9 months with additional timer

TABLE 2.--RECEIVER CHARACTERISTICS

Frequency	32 MHz
Type	dual conversion, crystal controlled
Bandwidth (3 dB)	3 kHz
Sensitivity	-123 dBm nominal for 10 dB S/N
Battery type	Nickle-cadmium, 225 mAh
Size	3 x 7 x 8 inches
Weight	2 lbs
Battery life	10 hours between charges

TABLE 3.--SYSTEM RANGE WITH VARIOUS RECEIVING ANTENNAS

<u>Antenna Type</u>	<u>Antenna Gain</u>	<u>Use</u>	<u>System Range*</u>
Loop (11" dia.)	-10 dB (est.)	on foot from aircraft	2 miles 20
Dipole (reference)	0	--	
Quad	5	field station	10
3 element yagi	7	field station	10
5 element yagi	9	base station	15

*Typical value -- varies widely with terrain

The yagi and quad antennas that were used for longer distance tracking had relatively broad patterns (45° to 60°), but bearing accuracy on the order of a few degrees could be obtained by rotating the antenna until the signal disappeared on either side, then bisecting the angle formed by the fade-out points. The slightly reduced accuracy of the larger antennas in comparison to the loop was not especially troublesome, since the long-distance bearings taken with the large antennas were usually intended only for rough location purposes before moving in on the animal with a portable receiver.

Normal tracking procedure was to record a signal from an instrumented grizzly at the base station using the 5 element yagi antenna. The direction of the signal source was plotted on a topographic map. A second and frequently a third bearing was made with the mobile unit. The intersection of the bearings generally fixed the animal's position to within a $1/4$ to $1/3$ mile area on the map. We then hiked to within 2 to 4 miles of the fix and activated the portable receiver.

When within range of the animal, we took a bearing by rotating the loop antenna of the portable receiver until a null was obtained. A null occurs at right angles to the plane of the loop and indicates that the animal is on a bearing bisecting the loop. The pattern of the loop antenna is symmetrical, so an ambiguity in the direction of signal arrival remains after the directional bearing is established. This ambiguity is resolved by activating the sense antenna, which is a vertical whip mounted next to the loop (Fig. 3). The sense antenna

suppresses one lobe of the loop antenna pattern and gives a non-symmetrical pattern from which the direction of signal arrival can be determined (Varney 1971). Thus, an increase in signal strength from the nonsymmetrical pattern enabled us to determine the source of the signal and move toward the instrumented animal; a decrease warned us that we were headed in the wrong direction.

As the instrumented animal was approached, the signal strength increased so that, at about 1/4 mile, a null became difficult to obtain. The receiver sensitivity setting was then altered to reduce the signal strength and get a null; the remaining distance to the instrumented grizzly was covered by following the null. Signal volume provided a good indication of distance between the bear and the observer. Using the portable receiver in this way, we frequently approached grizzlies to within 100 feet without disturbing them. The average distance at which we "jumped" them from daybeds in dense timber and windfall was 125 feet.

Locating grizzly No. 150 on 10 October 1964 was typical of our tracking operations. Hiking toward a previously established fix, the grizzly was located and "jumped" 8 miles from our base station and 3 miles from the field station where the signal bearings were taken. The bearing from base was 2.5° in error. The base receiving station was 120 feet lower than the grizzly and there was a 200 foot timbered ridge between the base station and the instrumented animal. In spite of this shielding ridge, grizzly No. 150 was successfully located on

this and other occasions. Both bearings and field fixes were made almost daily on this animal for several months.

Because of varying field conditions, some variations in the strength of the signal transmitted by different collars, and occasional equipment problems, we found that successful radiotracking required considerable judgment by the equipment operator. This judgment improved with field experience. Normally operating equipment, used by inexperienced personnel, did not always produce successful results.

Grizzly bears that we planned to track to dens were generally instrumented in late summer or early fall. These animals were radio-located almost daily either from the base station or in the field. When location data showed that an animal had moved from a bedding area or center of activity, we moved in on the animal using the portable receiver in order to make visual observations. Instrumented animals were followed on prehibernation treks to denning areas whenever possible; however, at such times the bears were not closely pursued. Our main objective was to maintain radio contact with the animal. We generally travelled the ridges to get better reception and on occasion bivouaced at elevated sites to continue monitoring throughout the night. If its nocturnal travels had carried it beyond the range of our equipment, this procedure enabled us to relocate the animal quickly the next day by moving in the direction of the last signals received.

We found it was not unusual for some grizzlies to move 10 to 15 miles during a 12-hour period. When this occurred in rough terrain

and the animal continued to move, it required anywhere from several days to a week of radio-searching to relocate the animal. In a few cases, when radio contact with a grizzly was lost during periods of extensive movements, it was not relocated. However, without exception, such animals were recaptured the following spring and the collars removed and/or replaced.

In general, the grizzlies adjusted well to the radio collars and did not attempt to remove them. Occasionally an animal would lose its collar, especially if it was one placed on the bear early in summer because we fitted such collars loosely to allow for an increase in weight and neck diameter without causing discomfort. Collars lost in this manner were easily retrieved. For instance, a transmitter collar removed by a grizzly but still operative was recovered by following a signal bearing made from a distance of 9 miles. When 2 miles away, we used the portable receiver which guided us to within 15 feet of the collar where it was sighted and retrieved. Two other collars dropped by grizzlies were similarly recovered.

In rare instances light planes were used to locate grizzlies. The search pattern consisted of flying to the point of last radio contact and monitoring the terrain in ever-widening circles. When we heard a signal, we utilized a combination of antenna nulls and signal strength to indicate the necessary flight course. Once in the near vicinity of the grizzly, its approximate location could be determined by an increase in the audio signal to peak volume as we flew over the

animal and a gradually fading signal as we passed over and beyond. By dropping to an altitude of 500 to 1,000 feet, the exact position of the bear could be plotted on a topographic map. On one occasion an instrumented animal was sighted and, on another occasion, the location of the den was initially located from the air and then visually confirmed on the ground. Because of a high cost factor and the distance to the nearest airport, we made limited use of aircraft in our tracking operations.

RESULTS

Den Site Selection

The dens of six different grizzlies were located, some for consecutive seasons. Thus, 11 active ones were found and information was obtained on site preference, den size, and construction. All dens used by grizzlies were located while they were being constructed, or when bears entered them for their winter sleep.

Information on den site selection (Table 4) was obtained from monitoring and observing instrumented grizzlies in the fall of the year. In 1961 and 1962, we were unable to track the radio-tagged bears to their dens. However, the dates of hibernation (Oct. 29 and Oct. 21-22, respectively) were obtained by observing movements of grizzlies during snowstorms and the lack of tracks thereafter. Later, with improved equipment, tracking grizzlies became routine, and we obtained specific dates when they entered dens to remain for the winter (Table 5).

TABLE 4.--CHARACTERISTICS OF ACTIVE GRIZZLY BEAR DENS

Designation of Grizzly No.	Sex	Year Den Used	Den Location	Vegetation Type	Soil Structure	Den Elevation (Feet)	Species of Den Tree	Den Measurements (inches)						Total Length	Den Lining	Fate of Den First Spring
								Chamber			Entrance					
								L	W	Ht	L	W	Ht			
164	F	1963*	Upper Alum Creek	Lodgepole Pine	Soft earth	8,200	Lodgepole	59	53	48	60	17	40	119	Conifer boughs	Remained intact
158	M	1964	Upper Trout Creek	Lodgepole Pine	Packed soil Gravel layer	8,400	Spruce	64	60	60	32	30	42	96	Conifer boughs	Remained intact
40	F	1964	Upper Alum Creek	Lodgepole Pine Spruce-Fir	Packed soil	8,200	Spruce	48	42	48	36	30	30	84	Conifer boughs	Collapsed
40	F(3)	1965	Upper Alum Creek Beach Lake	Lodgepole Pine	Packed soil	8,200	None	54	54	36	66	33	21	120	Grass Moss Rootlets	Remained intact
40	F	1966	Lower Trout Creek	Lodgepole Pine Spruce-Fir	Loose soil	8,000	Dead stump	60	85	28	30	17	20	90	Conifer boughs	Collapsed
202	M	1965	Yellow-stone Canyon	Spruce-Fir	Rocky (talus)	7,800	Log (1)	47	43	26	--	--	--	66	Conifer boughs	Remained intact
202	M	1966	Yellow-stone Canyon	Spruce-Fir	Rocky (talus)	7,800	Log	43	37	28	--	--	--	63	Conifer boughs	Collapsed
101	F	1966	Lower Trout Creek	Lodgepole Pine	Sandy soil	8,000	Whitebark Pine	54	48	30	12	14	36	66	None (2)	Remained intact
101	F	1967	Hedges Peak	Spruce-Fir Whitebark Pine	Packed soil Rocks	9,200	Dead spruce	63	56	40	45	15	54	108	Fir boughs	Collapsed
187	F	1967	Ice Lake	Lodgepole Pine	Packed soil	8,100	Whitebark Pine	--	--	--	36	21	27	--	None (2)	Collapsed
40	F	1968	Upper Trout Creek	Spruce-Fir	Packed soil	8,200	Spruce	68	54	30	38	24	--	106	Conifer boughs	Remained intact

(1) Attempted earlier to dig den at base of tree.

(2) Den abandoned before lining.

(3) Female pregnant.

* Signs of use the previous year.

TABLE 5.--DATA RELATED TO PREHIBERNATION BEHAVIOR OF GRIZZLIES

Designation of No.	Sex	Grizzly Age	First Recorded Den Digging	Final Movement to or Toward Den Area			Entering Den		
				Date	Weather Conditions	Temp. °F. Max. Min.	Date	Weather Conditions	Temp. °F. Max. Min.
164	Young, adult female	--	--	1963 November 4	Snowing, 4-6 inches on ground	36 28	November 5	Snow storm	31 16
150	Adult female with 3 cubs	--	--	1963 November 4	Snowing, 4-6 inches on ground	36 28	November 4	Snow storm	36 28
40	Female with cub	6-1/2	September 8 (2)	1964 November 1	Snowing, 12-18 inches on ground	45 32	November 10	Snow storm	40 24
158	Male yearling with 2 litter mates and adult	1-1/2	--	1964 October 29-30	Snowing, 12-18 inches on ground	58 38	November 10	Snow storm	40 24
40	Adult, pregnant female	7-1/2	September 3	1965 October 15-16	Snowing, 3-4 inches new snow	54 30 41 30	November 11	Snow storm	43 28
202	Weaned yearling male	1-1/2	October 27-29 No previous preparation	1965 October 15 Started moving	Snowing, 3-4 inches new snow	54 30			
				October 25-26 Completed move	No snow Clear	55 26 63 25	November 11	Snow storm	43 28
88	Weaned yearling male	1-1/2	After October 15	1965 October 15	Snowing, 3-4 inches new snow	54 30	Probably November 11	Snow storm	43 28
40	Adult female with 2 cubs	8-1/2	November 2-15 Some digging	1966 November 15	Snowing, 12 inches snow on ground	40 20	November 21	Snow storm	38 26
202	Young male	2-1/2	October 10-11	1966 November 6	Snowing, 5 inches snow on ground	38 29	November 21	Snow storm	38 26
101	Adult female with 1 cub	9-1/2	Some digging November 8	1966 November 14	Snowing, 10-12 inches snow on ground	45 24	Probably (1) November 21	Snow storm	38 26
120	Adult female	--	--	1966 About November 1	Snowing. Snow on ground	40 6	Probably November 21	Snow storm	38 26
187	Adult pregnant female	4-1/2	September 16	1967 October 27	Snowing	51 10	Probably (1) November 19	Snow storm	32 25
101	Adult female; 1 yearling	10-1/2	October 11	1967 October 27	Snowing	51 10	November 2-6 (2)		
101	Adult female; 1 yearling	10-1/2	November 7-11(2)	1967 November 2-6 moved to new den site	Snowing, 10-12 inches snow on ground	51 10	New den November 19	Snow storm	32 25
40	Adult female; 3 cubs	10-1/2	--	1968 November 2-3	Snowing, 10-12 inches snow on ground	-- --	November 3-4	Snow storm	-- --

(1) Den abandoned. New den not located.

(2) Den abandoned. New den located.

Over a 9-year period, these dates when grizzlies entered their dens to remain varied by as much as a month.

Bears of both sexes and several age classes were tracked to dens. These included 1 young adult female (barren), 1 young adult female with her first cub, 2 adult pregnant females, 2 adult females with cubs, and 2 adult females with yearlings (Table 5). Two young males were tracked to their dens, 1 as a weaned yearling and again as a 2-year-old -- the other as a yearling with his mother and 2 litter-mates. Very large boars were instrumented and tracked to denning areas, but none were successfully tracked to dens. Four dens of one female were located -- 3 of these in consecutive seasons; the dens of 2 other bears for 2 successive seasons (Table 5).

An orphaned grizzly, cub No. 78, was observed up to and soon after emerging from hibernation, evidence that cubs can survive the winter without parental care or guidance.

Grizzlies, whose dens were located, hibernated at altitudes ranging from 7,800 to 9,200 feet (Tables 4 and 6). All dens were located in timbered areas and all but one on northern slopes with the den entrance facing north. Couturier (1954) found that brown bears preferred a den that faced south. A north-facing den entrance appears to be advantageous to the hibernating grizzly in Yellowstone because prevailing southwest winds accumulate snow on northern exposures. The deep snow that accumulates in such locations insulates the den chamber from the extreme ambient air temperatures that may drop as low as -40°F .

TABLE 6.-- CHARACTERISTICS OF INACTIVE GRIZZLY BEAR DENS

Den Location	Vegetation Type	Soil Structure	Den Elevation (Feet)	Species of Den Tree	Den Measurements (Inches)						Den Lining	
					Chamber			Entrance				Total Length
					L	W	HT	L	W	HT		
Upper Trout Creek	Lodgepole pine	Hard, compacted	8,200	Spruce	43	63	43	64	26	26	107	Conifer boughs
Absaroka Range Mist Creek	Whitebark pine	Rocky	9,000	Whitebark pine	54	60	36	--	--	--	54	Conifer boughs
Lower Trout Creek	Lodgepole pine Spruce-fir	Loose soil	8,000	None	70	52	30	20	27	19	90	Conifer boughs
Yellowstone Canyon (North side)	Douglas-fir	Fine-rock soil	7,600	Matted vegetation	--	48	--	--	--	--	96	Den collapsed
Ice Lake Area	Lodgepole pine	Packed soil	8,100	Mat of <u>Vaccinium scoparium</u>	--	30	24	--	--	--	84	Den collapsed
Upper Trout Creek	Spruce-fir	Packed soil	8,200	Spruce	64	38	26	44	45	--	108	Partially collapsed

to -50°F . Also, there is less chance that snow on north slopes will melt during a warm period or winter "chinook". Water trickling into a den would appear to be disturbing and undesirable. Though early spring and late fall sightings revealed that grizzlies den throughout Yellowstone and beyond, all occupied dens were found in the central portion of the Park.

Dens were located relatively far from developed areas or human activity. For example, the winter dens of young male No. 202 were dug among rocks on a 45° talus slope in a nearly inaccessible part of the Yellowstone Canyon. Snow avalanches run down the canyon each spring. Large rocks periodically break from the cliffs and start small rock avalanches that have partly buried or have deeply scarred most of the trees on the slopes below. Small islands of timber have become established between the larger avalanche runs. However, even these do not appear to be a safe place for a bear to hibernate; yet No. 202 dug his dens in such spots. These dens were difficult to approach in summer and extremely hazardous to reach after the first snow.

Grizzlies seem to need and to seek isolation for the 6 months of their deep sleep. In the course of evolution, finding isolated den sites for hibernating would appear to be a factor favoring survival of the species. Primitive man and the American Indian undoubtedly found that grizzlies, lethargic until disturbed, were vulnerable in winter and the odds far more favorable for killing them during winter sleep than during their active period.

Den Construction

Most grizzlies prepared winter dens well in advance of the time they went into hibernation. The earliest recorded den diggings were on 3 and 8 September. The latest occurred 11 and 15 November; the bears completed these dens just in time to enter them for the winter (Table 5). In one of the latter cases, den construction had been delayed because the bear had abandoned her first den. The amount of disturbance needed to cause abandonment of a completed den or one under construction varied considerably with individual grizzlies. While dens were being constructed or occupied, we seldom approached closer than 100 feet, or remained for more than a few minutes. Nevertheless, No. 101 abandoned dens in two consecutive years (1966 and 1967), and No. 187 abandoned her's in late fall of 1967 in spite of these precautions. Measurements and photographs of the interiors of dens were made in the spring after the bears had left.

The den-digging dates shown in Table 5 record when excavating was first detected. The duration of den-digging varied, but usually the major excavation was accomplished within 3-7 days; minor digging activity occurred over a period of weeks. Interrupted radio signals enabled us to determine when bears were digging dens, and we then located and observed them (Craighead 1968). For example, in 1966, No. 202 returned twice to his den and, on each occasion, attenuated signals indicated he was digging; digging was visually confirmed on both occasions.

Jonkel and Cavan (1971) state that the base of a hollow tree was the site most often used for denning by black bears. These dens were within, not under the trees.

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Natural shelters were not utilized as dens by grizzlies, though matted windfalls and rock caves were available. All the dens we located were dug by grizzlies (Table 4). This is in contrast to the European brown bear which often uses natural shelters (Couturier 1954). Seven of 11 dens (Table 4) were dug at the base of trees; three at the base of stumps or with entrances beneath horizontal logs; one den was in the open. Erickson et al. (1964) found that most black bears dug dens beneath objects (such as logs or stumps) or into hillsides. No mention is made of dens excavated beneath trees. The Yellowstone grizzly frequently digs a den entrance at the base of a tree, and tunnels in through the large downward and outward sloping roots (Figs. 4 and 5). The roots limit the size of the den opening and may form a ceiling. Although grizzlies do not always select the base of a tree for den sites, such sites are preferred. Exceptions were No. 202, who dug his dens under horizontal logs (Fig. 6). However, this young grizzly made several attempts to dig dens at the bases of large trees; apparently he could not remove large rocks and boulders wedged between the roots. No. 40 was also unsuccessful in digging a den at the base of a large fir tree. She never completed the den, perhaps because the space between major roots was 8-10 inches too narrow for a den opening.

We believe it is instinctive for the grizzly to dig a den rather than appropriate or modify a natural cavity; some behavior supports this. For example, in the fall when grizzlies dig dens and gather boughs for beds, they also dig to cover carrion or kills more frequently than at



Fig. 4. Den excavated at base of tree. Roots frequently limit size of the entrance.

Fig. 5. Nearly vertical den entrance with den chamber lying directly beneath the tree.



other seasons of the year. In addition, when they move to their dens prior to hibernation, they perform a stereotyped "housecleaning" by digging inside and outside the den. This seasonal increase in digging may reflect a biological drive. The fact that some den digging occurs long before the grizzlies enter their dens for winter and at a time when there is no immediate need for a den suggests that this behavior may be triggered by hormonal changes (Fig. 7).

Dens of grizzlies were just adequate for the number of bears sheltered, whether an individual or a family. Females with cubs as well as females with yearlings slept in the same den in close contact with their offspring. The dens were usually constructed with an entrance way leading into the bed chamber (Fig. 8). The average size of this chamber (determined from 10 dens) was: 56 x 53 x 37 inches. A den which sheltered No. 39 and her 3 yearlings was almost as wide as it was long. In 1966 when No. 40 hibernated with 2 cubs, her den was wider than it was long, and the 3 bears slept curled side by side (Table 4). Females with cubs or yearlings dig wider dens than bears that hibernate alone. Den entrances went directly into the chamber, or had entrance tunnels as long as 66 inches. Width of den openings varied from 14 to 33 inches and averaged 22; heights ranged from 20 to 54 inches and averaged 34. Den openings impressed us as being small for the size of the animals using them. In some instances, it appeared that even a medium-sized bear would have had difficulty squeezing through the opening to the chamber. Length of bed chambers and the entranceways combined averaged 92 inches. The



Fig. 6. Den constructed under a horizontal log on a steep talus slope. The first den of grizzly No. 202.



Fig. 7. Female No. 40, in lethargic condition, moving to den. Dens were located in 1964, 1965, 1966, and 1968.

small size of these chambers is functional, i.e., body heat from the bears substantially modify den ambient temperatures (Craighead et al. in press). Dens never contained more than 1 chamber; alcoves, such as those reported for the polar bear (Harrington 1968), were not observed.

After we located active dens by radiotracking grizzlies, a general pattern of den site preference emerged which enabled us to seek for and find dens used in previous years. The size and characteristics of six such dens are shown in Table 6. These were constructed by unmarked grizzlies and were not in current use. Inactive dens, like active ones, were on north-facing slopes, in dense timber, in secluded areas, and in five of six instances, were dug at the base of large trees. The average bed chamber measurements of 52 x 50 x 39 inches are similar to those of active dens. The greatest length of a den chamber and entranceway was 108 inches (Table 6). A natural rock cave located in Yellowstone Canyon at 7,800 feet measured 87 inches long and had a den chamber 33 x 57 x 36 inches, and was lined with boughs. It appeared suitable for a den, but was not used and probably served only as a day bed.

Den Environment

Den beds were usually composed of spruce or fir boughs, 3 to 14 inches deep (Fig. 9). Normally boughs were chewed from spruce or fir trees growing within a radius of 50 feet of the den. During three winters when female No. 40 was not pregnant, she used conifer boughs, but when



Fig. 8. Den entranceway excavated through obstructing roots which were chewed off by bear. Photographer was in den chamber and observer outside looking in.

Fig. 9. Den lined with conifer boughs. Linings in different dens varied from 3-14 inches. When grizzlies emerged from hibernation some did not disturb the bed; others raked the bedding material out of the den.



pregnant, she prepared a bed of moss and grass. Pregnant females may routinely use fine, soft material for beds. Dens are usually lined soon after they are dug, but in one case, a grizzly accumulated a large pile of boughs prior to bed construction and left them outside the den entrance. The bough bed prepared by grizzly No. 202 was circular with a cuplike depression (Fig. 6). The diameter across the top of the depression was 31 inches. When measured following winter use, the bed was 12 inches deep. It was probably 16-18 inches deep when first constructed. From the size of the bear and the den, we inferred that the yearling slept with his head and shoulders protected but the rest of his body exposed.

All dens were situated where the entranceways would fill with snow, forming a sealed chamber with little transfer of air (Fig. 10). Occasionally a bed was elevated above the entranceway; this created a heat trap that prevented the air warmed by the bear's body from escaping before snow filled the entrance (Fig. 11). We do not know whether a den of this type is constructed accidentally or is the result of instinctive or learned behavior. However, it may be instinctive for grizzlies to construct a heat trap when conditions for doing so are favorable. The den of the grizzly bear is a very localized environment with temperatures warmer and more constant than those existing outside. In addition, when a deep insulating layer of boughs is used, many "dead air" pockets form a microclimate next to the bear within the porous, bedding material. Here, the temperature is considerably warmer than the

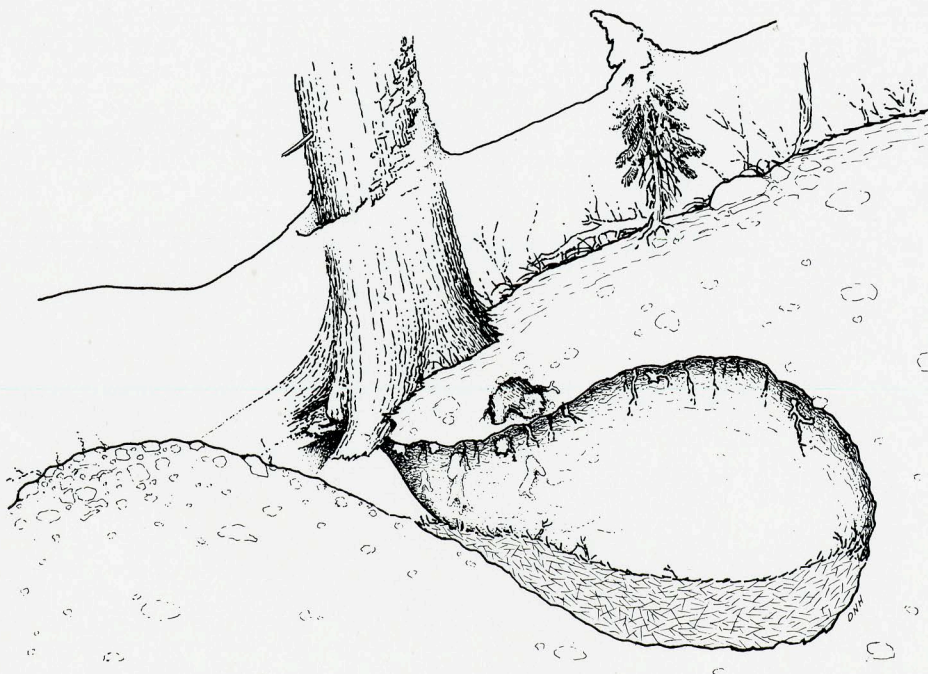


Fig. 10. Den with bed lower than entrance. Such dens were covered with five to ten feet of snow.



Fig. 11. Den constructed so the bed lay slightly above the entrance; this helped to provide a constant den temperature by forming a dead-air space that functioned as a heat trap until deep snow sealed the den entrance.

general ambient temperature of the den chamber. Thus, a very narrow "envelope" of bedding and air lies between a bear and its den.

The temperature of such a microclimate in a black bear den was recorded by placing a thermistor probe from a body temperature transmitter between the bear and his bed of dry pine needles and finely shredded twigs and rootlets (Craighead and Craighead 1966). The maximum recorded temperature for the microclimate of $97^{\circ}\text{F.} \pm 2^{\circ}\text{F.}$ closely approached the body temperature of 101°F. recorded for an active bear in summer, and exceeded the average rectal temperature (96°F.) of a hibernating black bear which was monitored for 4 days (Craighead et al. in Press). However, over a 55 minute period the temperature fluctuated between 97°F. and 83°F. The maximum temperature of 97°F. occurred when the temperature sensor was against the bear's body, perhaps where his fur was thin and heat conduction was efficient. The bear was awake and moving within the den. Thus, at this time his body temperature was probably close to 100°F. The thin layer of dead air and bedding between the bear and his den enveloped approximately $3/4$ of the bear's body surface when he was curled in repose. The insulated bed was 30 inches in diameter, 18 inches deep and cuplike, with nearly perpendicular walls which fitted the bear snugly and minimized temperature changes (Fig. 12). Bed materials differed from those used by grizzlies, but the dimensions and structure of the bed were similar to those prepared by yearling grizzly No. 202. Our observations of both black and grizzly bears in their dens have shown considerable variation among individual animals in

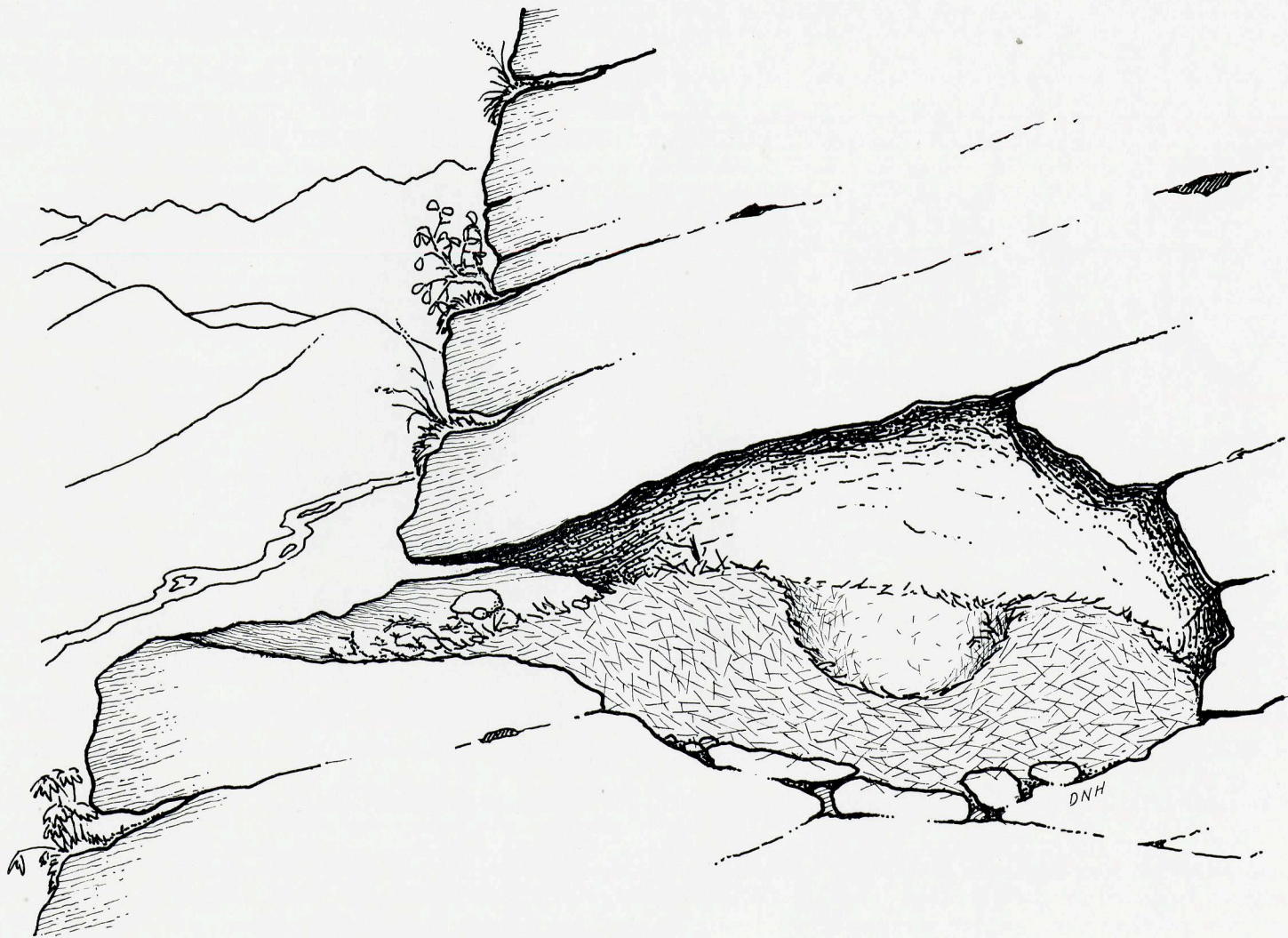


Fig. 12. Black Bear Den
A natural cave with a bed 18" deep and 30" in diameter.

degree of lethargy. The microclimatic temperatures surrounding a black or grizzly bear in winter sleep are governed by the temperature of the bear, the temperature of the den wall, and the insulating qualities of the bedding material. The dormancy temperature may, in turn, be influenced by the temperature of the microclimate enveloping the animal. Thus, winter dormancy and the degree of lethargy of wild bears may show individual variation directly related to the microclimatic temperatures.

Distances Traveled to Den Sites

Distances traveled by instrumented grizzlies moving to their dens or den sites from fall or summer foraging areas varied from 2.5 to over 30 airline miles (Table 7).

Observations of color-marked grizzlies, made when they dispersed to den sites in the fall, revealed that some grizzlies traveled even greater distances than did those we were able to track by radio. Some traveled beyond the boundaries of Yellowstone National Park.

Distinctions Between Daybeds and Dens

In the Yellowstone region, most grizzlies are active both day and night during the early spring months when food is relatively scarce. They are again similarly active during the fall of the year when they forage prior to entering dens for the winter. In summer, they rest during daylight hours and forage at night. They seek windfalls and dense thickets of spruce, fir, and lodgepole pine in which to rest. Here they

TABLE 7.--DISTANCES GRIZZLIES TRAVELED FROM FALL OR SUMMER FORAGING
AREAS TO DEN SITES

<u>Grizzly Number</u>	<u>Airline Distance Traveled</u>
40	5.1
40	5.5
40	5.5
40	6.8
101	2.5
101	11
202	8
202	8
187	11
39	5
14	16
164	14
7	14
34	16+
150	6
96	30+
76	21+

excavate daytime beds or lairs, most of which vary in depth from 1 to 18 inches. Forest duff is often scraped to mineral soil. Occasionally daybeds, like winter beds, are lined with grass, pine needles or other vegetation. Most beds are shallow excavations, but at times denlike burrows are dug 3 or 4 feet into slopes or under fallen logs; these burrows are cooler than surface beds.

Burrow-type daybeds can be mistaken for winter dens, and occasionally a den such as that of No. 202 can resemble a daybed (Fig. 6). However, daybeds are usually located relatively close to feeding areas, may be visited and used by different bears, and they are not necessarily constructed into north-facing slopes nor at the base of large trees. They may function as retreats during the breeding season. In 1964, a large boar and a female in estrus were located in daybeds 25 feet apart. The female had dug a burrow several feet into a hillside. With her body in the burrow and her head and muzzle resting on the tailings from the cave, she could discourage unsolicited attentions from the male. Daybeds, used during the pre- and post-hibernating periods are normally clustered around a den, but even the most elaborate of these are easily distinguished from the den itself.

Relation of Den Site to Home Range

Two types of grizzly bear home ranges were plotted and delineated by radiotracking. One was a distinct, well-defined area used throughout the year. The other type of home range consisted of a summer and early

fall foraging area, connected by a migratory corridor to an early-spring and late-fall area that contained the den. The home range of an animal provides all the essentials of life, and thus by definition, includes its den site. Den site selection and prehibernation behavior influence range size and pattern, and conversely, home range characteristics affect the choice of a den location.

We observed some interesting prehibernation behavior, related to home ranges, while radiotracking grizzlies. During the fall of 1965, No. 202 was closely monitored. On 25 October, he left his regular summer range, swam the Yellowstone River, and traveled directly north and then east to a site in Yellowstone Canyon where he subsequently dug his den (Fig. 13). When he crossed the Yellowstone River, this weaned yearling left the summer range he had inhabited. Except during his spring move from the natal den and his return the ensuing fall, this young bear had spent his entire life in the immediate vicinity of Hayden Valley. He dug his first den within a few days of selecting the site (Fig. 6). It was within the known home range of his color-marked mother, female No. 65; her home range had been determined by observation over a period of years.

In comparison to No. 202, No. 188, a weaned grizzly, also established a summer range within the home range of his mother, female No. 40. This yearling had also spent all his life within the home range of his mother. We thought he might hibernate within this familiar territory, but during a snowstorm in late October, we followed him into new and distant terrain; apparently he was seeking a hibernation site. He



Fig. 13. Denning area of yearling grizzly No. 202 in the canyon of the Yellowstone River in 1965. In spite of the rocky terrain, the den was completely excavated by the animal. Isolation provided by the canyon in this case, and by remote timbered areas in other instances were characteristic of denning areas.

Fig. 14. Observer standing in entranceway to show steep slope of entrance to den which had an elevated bed chamber and heat trap. Note excavated soil in right-hand, lower corner of photograph.



outtraveled us in the storm; we lost his signal and were unable to pick it up again. From observations made in later years, we determined that he established a home range consisting of a summer range with a migratory corridor to a fall range where he denned. Thus, his home range was very different from that of his mother. Such prehibernation dispersion during the fall by young grizzlies, disassociated from parental protection, is a common occurrence. At this time, they establish a home range and adjust to an independent life.

Re-use of Dens

Old bedding material found in a debris pile at the den where No. 164 wintered during 1963 suggested that this den might have been used the previous year (Fig. 14). Grizzlies No. 40 (1966) and No. 101 (1967) raked the bedding out of their dens before leaving them in spring. This suggested that they would re-use them; however, these dens and others to which we radiotracked grizzlies were never re-used. Five dens collapsed when the soil became saturated with water in late spring, and thus were not suitable for re-use (Fig. 15); however, six remained intact (Table 4) and could have been reoccupied, but were not.

In 2 consecutive years, grizzly No. 202 dug two dens only 300 feet apart. His first den was poorly excavated and probably inadequate for re-use the following year. The second-year den was a decided improvement; the grizzly removed an estimated ton of rock in preparing it. Although we believe that the biological drive to dig a den is instinctive,

a learning process is involved, and den construction improves with experience. Near many active den sites, we found evidence of former dens (Fig. 15). Three collapsed dens were located very close to the active den of grizzly No. 164. A collapsed den within a few hundred feet of the den of No. 40 (1966) had plant growth on the debris pile indicating that it was at least 5-7 years old. It could possibly have been constructed by No. 40, but more likely had been constructed by another bear. We had other indirect evidence of the use of a denning area by more than one bear, but never did two animals dig separate dens in the same area in the same season. Possibly the characteristics of a good denning area are recognized by bears and the site attracts the same bear for a number of years or other bears at different times.

We found no evidence that any of the animals we radiotracked to dens died during the winter. Nevertheless, we suspect that old bears may die in or near their dens, because we made a number of observations of very old, color-marked bears in the fall that were never again observed.

Prehibernation Movement and Behavior

In the early years of the study (1960-61), we observed that grizzlies moved to their dens during a snowstorm and that tracks were not visible anywhere in the area after the storm. This suggested that certain environmental stimuli may have triggered all or most of the grizzlies to move to and enter their dens simultaneously. Through radiotracking, we learned that some bears dug dens long before they were ready to hibernate.



Fig. 15. A den which caved in after use. This and similar dens were found in the vicinity of a new den dug by grizzly No. 164. This may indicate the return of this bear to a specific area to den, or the attraction of other bears to a "prime" denning area in previous years.

Fig. 16. Bough bed constructed on the snow in March several hundred feet from the winter den. Female No. 40 and her offspring used these beds for several weeks before leaving the area of their den. Other bears did not construct such beds.



They periodically returned to these dens and enlarged them following early season snowstorms. If a period of warm weather followed, grizzlies usually returned to their fall foraging areas until another storm sent them denward again. However, in some cases, they moved to their dens during snowstorms and remained there until a subsequent snowfall and low temperatures put them in for the winter. In 1961 and 1963, all the grizzlies we had under observation moved directly from fall foraging areas during a snowstorm and entered their dens for the winter (Table 5).

On the clear and mild morning of 15 October 1965, the barometric pressure began to fall, and No. 40 started to move. By late afternoon, a severe snowstorm was in progress, and we radiotracked her to the den. This and similar behavior of other grizzlies suggest that they may be able to detect approaching storms, possibly by variations in barometric pressure or through sensitivity to infrasonic waves (Green and Dunn 1968). Some such stimuli appear to initiate movements to dens before storm signs are visually apparent.

Grizzlies living under the same environmental conditions entered their dens at the same time during a storm regardless of whether they were waiting close to their dens (the case of No. 40 in 1965) or were foraging at some distance. At the time of entering dens, minimum ambient air temperatures as well as maximum temperatures in shaded den sites were below the freezing level. From 1963 through 1968, we never found tracks throughout extensive areas where grizzlies had been roaming and foraging prior to the storms that put them in their dens. The nearly simultaneous

entering of dens during falling snow conceals tracks that could reveal the den locations. This behavior may have survival value for the species. However, black bears in Yellowstone generally enter dens earlier in the season, and their dates of entry are varied. In 1966 black bear No. 1 entered its den on 3 October, and an unmarked bear entered its on 6 November. In 1967, No. 1 entered 2 October, and No. 3, 29 October. In 1968, No. 5 entered 26 October, and No. 1, 9 September. The signal from No. 1 was lost, so it is possible that the bear did not remain in the den at this early date. However, the bear was not observed again during the fall of 1968. During a snowstorm on 15 October 1965, No. 202, a weaned yearling grizzly, left his summer and early fall foraging area and moved 4.5 airline miles into new territory where he foraged and appeared to be seeking a den site. He remained there until 25-26 October when he moved 12.5 miles during clear weather and started digging what was to become his den (Table 5). This is the only instrumented grizzly whose final move to a den was not made during a snowstorm. However, No. 202 did not enter his den for the winter until a major snowstorm arrived on 11 November.

In 1961, the grizzlies hibernated on 21 October, the earliest date recorded. Snow and low temperatures occurred early in the fall and continued with few breaks until the bears hibernated. The first snowfall of 3-4 inches occurred on 11 September and was followed by another snowfall of 4-5 inches on 18 September. The average minimum temperature for September was 29°F., and the average maximum, 51°F. The

October 1961 average minimum and maximum temperatures were 22°F. and 45°F. It is perhaps significant that the most "wintery" fall period coincided with the earliest hibernation date.

A combination of low temperatures and snowstorms appears to condition the bears and eventually influence the time at which they enter their dens. A convenient food supply, little snow, and relatively high ambient air temperatures tend to delay hibernation. On the other hand, available food will not deter bears from entering their dens if snow is accumulating on the ground and snowstorms and severe cold occur at the same time. In the cold fall of 1961, when the grizzlies hibernated during a snowstorm on 21-22 October, the whitebark and limber pines produced very few nuts and the meadow mouse (Microtus sp.) population was low. In general, food was probably less abundant than in most other years. However, in October, a number of marked and unmarked grizzlies feeding on an elk carcass in Hayden Valley abandoned this food supply and moved to their dens during a snowstorm.

In 1966, with snow on the ground, grizzlies No. 40 and No. 101 and their families left their den sites and visited the sparse remains of a bison carcass. This food supply, within a relatively short distance of the two dens, apparently influenced the prehibernation behavior of these animals. We expected them to remain within a hundred yards of their dens as other grizzlies had done, but instead, they daily moved a mile or more to the carcass and back to their dens, leaving well-worn trails. However, when a severe snowstorm occurred on 21 November, both

families entered dens for the winter.

Over a 9-year period, the onset of hibernation varied by as much as a month. It therefore appears that change in light as winter approaches is not a factor influencing the exact time of hibernation for grizzly bears. Hock (1955), working with Citellus undulatus and studying the different climatic and ecological factors that may influence hibernation, found no relationship between the beginning of hibernation and the temperature, snowfalls, or the availability of food. The only close correlation he observed was between illumination and hibernation. Thus, the "triggering mechanism" to initiate hibernation may be different in ecological and physiological hibernators.

During the summer of 1966, instrumented grizzly No. 40 and her two cubs established a close relationship with female No. 101 and her cub. This close relationship extended throughout the summer and continued until the families entered separate dens. The association appeared to have altered their normal denning behavior. Instead of returning to her former hibernation site near upper Alum Creek, No. 40 dug her den near upper Trout Creek; her den was only 1.5 miles from the den of No. 101 (Table 4). The usual denning areas of these two females were approximately 16 airline miles apart. Instead of remaining close to their dens, the two families visited back and forth between dens and appeared reluctant to terminate the summer relationship. The prehibernation behavior of these bears was contrary to that observed in all other grizzlies, who sought solitude for themselves and families. The

relationship, however, provided greater security for the young of both families and was continued, though modified, the following spring when No. 40 weaned her yearlings and bred, while No. 101 kept her yearling and adopted the 2 yearlings weaned by No. 40. Such a practice would tend to increase productivity by allowing one of the two females to come in estrus a year sooner than otherwise possible. It also benefits the survival of yearlings, a relatively vulnerable age class.

Prehibernation Lethargy

In the late fall of 1965, we noticed a distinct lethargy in all grizzlies closely observed prior to hibernation. For example, on 14 October, we found instrumented grizzly No. 188 in a daybed. As we approached, he moved away slowly but soon stopped and sat down. Within a few minutes, his head began to sway, and he slumped forward with his muzzle on the ground turned inward under his body. Although aware of our presence, he could not remain awake and alert. He made a number of attempts to raise his head and rise from his sitting posture, only to slouch forward with his muzzle tucked between his legs. We moved to within 100 feet before he rose and lumbered off. Similar behavior occurred when we observed instrumented grizzly No. 202 on the same day.

About 2 weeks later on 3 November, lethargy was even more pronounced. No. 202's radio signal led us to the edge of the Yellowstone Canyon. A 3-bearing fix placed the grizzly directly below us. While we scanned the terrain with binoculars, the crash of a dislodged rock brought

a roar from the grizzly lying just below. For a half hour he remained nearly motionless in a sitting-fetal posture. He appeared to be in advanced lethargy and apparently never detected us.

On 25 October 1965, we approached to within 30 feet of No. 40 in her den. She was sufficiently lethargic that our presence did not disturb her. In this condition, she either stayed close to her den or within it. This behavior continued until 11 November, when she entered the den during a snowstorm to remain for the winter. She had moved to her den site a full month before finally denning for the winter. We suspect that early onset of lethargy influenced this movement.

The lethargic condition of these bears during the fall of 1965 was comparable to the condition of lethargy that they normally attained after entering their dens to winter.

Eisentraut (1960) noted that, with protracted exposure to cold, the higher, warm-blooded animals can go below the lower threshold of activity and a hypothermic lethargy ensues. This did not appear to be the case with the grizzlies under observation. During previous fall periods with more prolonged cold, they did not exhibit lethargy prior to entering dens.

Quite possibly weather conditions in the fall of 1965 initiated lethargy early in the season and affected grizzly prehibernation behavior, and movement to den sites. An early fall period of snow and unusual cold occurred from 15 through 28 September. The minimum temperature for the 18-20 September cold spell was 7°F. This was the earliest period

of snow and low temperatures experienced in the course of the study. Ambient air temperatures were lower than at the November 1965 time of hibernation (Table 5). Four to 6 inches of snow covered the ground in the central portion of the Park, and snow was deeper at higher elevations. This cold spell was followed by warm, mild fall weather. The combination of early snow and low temperatures did not stimulate grizzlies to hibernate, but it did disperse some from summer to fall foraging areas, and appears to have been a factor triggering hibernation processes so that the bears became lethargic and physiologically ready to hibernate by late October, before the usual environmental stimulus of a "final" snowstorm caused them to enter their dens for the winter on 11 November. Although lethargy occurred earlier than in other seasons, the grizzlies did not enter and remain in their dens until the 11 November date.

Defense of Dens

Information obtained with and without the use of radios indicate that the Yellowstone grizzlies are not territorial. On a number of occasions we have observed more than 20 grizzlies at one carcass feeding together with surprisingly little friction. We have never observed the defense of a home range or compensatory movements (Craighead and Craighead 1956) or mutual avoidance (Hornocker 1970). We thought that if grizzlies defended specific areas, these areas most likely would be in the vicinity of their winter dens. Here they might also attack a man. However, we observed no overt defense of a den or den area against either

man or other grizzlies. On one occasion when we were very close to the den of No. 158, our radio signal indicated that she and her family were moving toward us through dense, "doghair", lodgepole pine. Immediately after climbing trees, our signal revealed that the grizzlies were running away; apparently they had detected us.

In the fall of 1967, we approached to within 200 feet of the den of grizzly No. 101. The radio signal showed she was inside. We moved on without disturbing her. Several hours later we returned and saw fresh bear tracks leaving the den and got a faint signal on our radio receiver. We followed the tracks for a half mile through knee-deep snow. Signs showed us that, after leaving the den, No. 101 crossed our trail. When she did so, she started running and urinating and the urine trail persisted for about 200 yards. We interpreted this as a physiological manifestation of fright. The female abandoned the den. Later in the season when her newly dug second den (Table 5) was approached, she growled threateningly, came out of the den, and retreated a short distance. We observed similar behavior at the dens of grizzlies No. 40, 164, 202, and 187.

Visits to Dens During Winter Sleep

On 28 December 1966, we visited the den of grizzly No. 40 and her two cubs of the year. The den was located on a steep slope, and we had to approach it from below on snowshoes. We could see that the den entrance was still open and that there were no signs to indicate the bears

had left the den since entering in November. While one man stood guard, the other slid head first down the inclined entranceway so he could peer into the den chamber. In this awkward position, he was approximately 5 feet from the sleeping female and her two grown cubs. All three grizzlies were lethargic and sleeping, but apparently the female detected our presence for she growled and shifted her position. We took some flash pictures and then quickly retreated. Although this aroused the grizzlies, they were sufficiently lethargic that they did not come out of the den, during the short period of time we were present, nor did they later abandon it.

The Yellowstone grizzly mates in June and early July, but a delay in implantation postpones embryonic development. The blastocysts probably implant between 15-30 December, about a month after the sows enter their dens (Craighead et al. 1969). Parturition occurs in late January or in February, but we have been unable to obtain specific dates. Radiotelemetry can, in the future, provide information on the length of the delay period and physiological parameters of parturition.

No feces or traces of urine have been found in recently abandoned grizzly bear dens, or even observed close to them. Harrington (1968) found that polar bears usually keep their dens clean; only traces of urine and minute fecal fragments were found in six of nine dens he examined. We have found neither feces nor urine in six, active, black bear dens visited while the bears were in winter sleep. Three dens were examined after immobilizing and removing the bears; all six dens

were inspected in the spring after the animals left. We observed black watery excrement, passed by grizzlies prior to entering winter dens; this suggests a scouring and cleaning of the alimentary tract. The Yellowstone grizzlies normally fast from the time they enter their dens until they leave them in the spring.

Occasionally a grizzly emerges from its den in midwinter. One, in the Old Faithful area, came out in the latter part of February 1967 and was observed on the carcass of an elk that had either been killed or had died in the vicinity of the den.

Emergence From Hibernation

Bough and bark beds laid on the snow near the den of grizzly No. 40 and her yearlings in 1965 (Fig. 16) indicated that they had emerged from the den in late March but did not leave the den area until about 20 April. The beds were on different snow strata or levels, indicating time intervals between construction. Close examination of the beds showed that the bears must have slept on them and been covered by snow from subsequent storms. As the snow piled up over the sleeping animals, their breathing produced air shafts to the surface. In 1967, No. 40 emerged from hibernation with another family of yearlings but on this occasion left the den area without building bough beds. Other grizzlies emerged from dens 3 to 4 weeks before they left their den sites. When grizzlies first emerge, the snow is frequently too soft and deep for them to travel, and they remain at the dens until warm, sunny

days, followed by chilly nights, crust the snow so it will support their weight.

Grizzlies may be induced to emerge from dens before they can travel because air temperatures in early spring, during the day, are often warmer than those within the den. At 10:45 A.M. on 28 April 1965, the air temperature inside the den of No. 40 was 32°F. The air temperature in the shade, outside of the den and 3 feet above the snow, was 40°F. The ambient air temperature in the sun was 50°F.

Our observations reveal that mature male and female grizzlies tend to leave den areas earlier than females with yearlings. Females with cubs of the year are the last to leave den sites and some may remain in the vicinity of the den until the snow has disappeared.

The carcasses of winter-killed animals form a considerable portion of the diet of grizzly bears in early spring. In addition, grizzlies kill those weakened by a severe winter. Our records include observations and authentic reports of grizzlies killing full-grown moose, bison, and elk. In most cases the animals were attacked in deep snow, while crossing rivers, or when otherwise handicapped or incapacitated. Some were so close to death from malnutrition that they made no attempts to evade attack. We have a number of sight records (our own and others) of two or more grizzlies pursuing and killing elk in well-coordinated attacks. The majority of elk and bison carcasses that were utilized by grizzlies were in advanced stages of malnutrition as evidenced by bone marrow tests. The same was true of

most of those that fell prey to bears (Craighead and Craighead unpub.).

A late spring with deep snow on the ground, such as occurred in 1970, can produce a higher than normal number of starving ungulates which fall prey to hungry grizzlies. Such predation is atypical, and the fundamental cause of death is malnutrition, not predation.

Our observations indicate that the grizzly's role as a carnivore, prior to and immediately after hibernation, in Yellowstone is first a scavenger, second a predator on small prey species (especially when these are at high densities), and last, a killer of large prey animals.

Summary

Over a 9-year period, grizzly bears were studied by means of radiotracking. Eleven active dens were located. Den selection and digging may occur as early as 3 September. Dens were dug entirely by the grizzlies, and no natural shelters were utilized. Dens were not large, and all bed chambers were lined with boughs. Dens located by radio were not reused, but circumstantial evidence suggested occasional re-use. It appears that den digging is instinctive behavior for the grizzly, and is reinforced by experience. Grizzlies traveled from fall foraging areas to den sites over distances varying from a few miles to 30 or more. Each year, grizzlies living under the same environmental conditions hibernated at about the same time. The dates when grizzlies entered dens for their winter sleep were influenced by environmental factors and, during 9 years, varied by as much as a month.

The bears entered their dens during snowstorms, This eliminates tracks and appears to have survival value for the species by protecting and isolating the grizzly during the period of its life when it is most vulnerable to man.

In the fall of 1965, a prehibernation lethargy was observed in grizzlies prior to entering their dens. This premature onset of lethargy appeared to have been activated by an unusually cold spell in September. When grizzlies emerge from winter sleep, winter-killed ungulates are major items in their diet.

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