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FACULTY OF GRADUATE STUDIES

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FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

of

CHARLES JONKEL

B.Sc., University of Montana, 1957

M.Sc., University of Montana, 1959

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THE ECOLOGY, POPULATION DYNAMICS, AND MANAGEMENT OF THE BLACK BEAR IN THE SPRUCE-FIR FOREST OF NORTHWESTERN MONTANA

ABSTRACT

This research was designed to study the ecology and population dynamics of black bears in the spruce and fir forest of northwestern Montana, to test the hypothesis that extrinsic factors caused fluctuations in population numbers, and to develop management principles for bears.

The rough topography and moderate to heavy precipitation on the Big Creek study area have created varied ecological conditions which in many ways are excellent for black bears. Seral and climax stands of the Picea-Abies/Pachistima myrsinites association are used most extensively by bears, but other vegetative types are important seasonally.

The home ranges of adult bears on the area are small and they remain the same size from year to year. As resident males mature, however, their ranges increase in area. Bears do congregate, but only where there is an overlap in their home ranges. Even then they do not form compact groups, but keep at least 50 yards (48 metres) between individuals.

Many adult females (bears approximately 4-1/2 years or older) do not have young, apparently because of the failure of females to ovulate, prenatal mortality, and early mortality. Tentative conclusions suggest that seasonal restrictions in nutrition delay the physical maturity and thereby the sexual maturity of some bears. These restrictions are caused by the climate of Big Creek and are detrimental even to adult females on certain years. Inadequate nutrition is also suggested by the observation that some yearlings inhibit estrus for two years by suckling up to 16 months of age. The nutrition of adult males and of many adult females generally is excellent, however. Litter sizes on Big Creek and throughout the West are smaller than in Eastern North America.

The survival of cubs is high (95 per cent) from 1/2 to 1-1/2 years of age while they are with their mothers, but all sub-adults are physically weak in late spring and natural loss is considerable among sub-adults 1-1/2 to 3-1/2 years old. They appear especially vulnerable to changes in climate, parasitism, predation, food quantity and quality, and the behaviour of adult bears. Many sub-adult males disperse from the area.

Annual changes in the density of bears on Big Creek are caused in part by man, by dispersal of sub-adults, and through changes in the reproductive success of adults and the natural mortality of sub-adults. The numbers of adults on the area remain relatively constant from year to year.

Even though food is unlimited during some seasons, a form of territoriality within "social groups" spaces the bears on Big Creek and ultimately exerts a definite control over density. The density is relatively high on Big Creek and probably results in more social interaction and territoriality than in bears elsewhere. Longer care of young, smaller litter sizes, and increased social organization all seem evident as reactions to the Big Creek environment. Extrinsic and intrinsic forces unite, therefore, in population regulation, and the net result is the creation of an excellent habitat for adult black bears, but an harsh environment for sub-adults after they have left their mothers.

GRADUATE STUDIES

Field of Study: Zoology

Animal Genetics	D. Suzuki
Advanced Ecology	D. Chitty

Invertebrate Zoology	P. A. Dehnel
Comparative Ethology	M. D. F. Udvardy
Directed Studies (Reproductive Physiology)	W. D. Kitts

PUBLICATIONS

Jonkel, C. J. 1959. An ecological and physiological stu of pine marten. Unpub. M.S. thesis. Montana State Univ., Missoula. vii + 81 pp.

Jonkel, C. J. and R. P. Weckwerth, 1963. Sexual maturi and implantation of blastocysts in the wild pi marten. J. of Wildl. Mgmt. 27(1):93-98.

Jonkel, C. J. and K. R. Greer, 1963. Fall food habits of Spruce Grouse in northwestern Montana. J. Wildl. Mgmt. 27(4):593-596.

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B. Sc., University of Montana, 1957

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A thesis submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

August, 1967

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Department of Zoology

The University of British Columbia
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Date August 28, 1967

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The survival of cubs is high (95 per cent) from 1/2 to 1-1/2 years of age while they are with their mothers, but all sub-adults are physically weak in late spring and natural loss is considerable among sub-adults 1-1/2 to 3-1/2 years old. They appear especially vulnerable to changes in climate, parasitism, predation, food quantity and quality, and the behaviour of adult bears. Many sub-adult males disperse from the area.

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Fletcher Newby of the Montana Fish and Game Department suggested this study and assisted in making the initial plans. Vernon Hawley, formerly with the Montana Fish and Game Department, and Richard Weckwerth, a management biologist with the Montana Fish and Game Department, both aided me considerably with comments and criticism in preparing the design of the study. Edward Tisch, Gary Gier, and James Rice assisted with the field work in consecutive years, and many individuals in the Whitefish and Columbia Falls, Montana, vicinity cooperated in many ways. Dean I. McT. Cowan has supervised my research since 1963 and helped me with suggestions and advice. The members of my committee: Dean I. McT. Cowan, Dr. D. H. Chitty, Dr. H. D. Fisher, and Dr. J. E. Phillips, all made valuable comments for the preparation of this thesis. I wish to express my sincere appreciation to all of these people.

The Montana Fish and Game Department financed the study through the summer of 1963 and during summers from 1964 through 1965. The University of British Columbia gave financial assistance from 1963 through 1966. Personnel of the National Park Service, the United States Forest Service, and the American Timber Company all aided the study in various ways. Without the assistance of these agencies the study could not have been completed.

PART I

GENERAL TOPICS

CHAPTER ONE

INTRODUCTION

This study was originated in northwestern Montana by the Montana Fish and Game Department to aid in the management of black bears (*Ursus americanus*, Pallas) as a game species. The study was begun in June, 1959, and continued through May of 1966. The study area selected was the Big Creek drainage 10 miles north of Whitefish, Montana. During 1959 and 1960 Tisch (1961) conducted a food habits study of the black bear in association with this study and in the same area.

In the years prior to 1959 the population on the Big Creek study area was believed to be high, and it seemed that although there was little hunting pressure, there were annual fluctuations in numbers. The way in which these observations relate to the regulation and maintenance of population numbers is important, especially since throughout much of North America the black bear appears to be as abundant as it has ever been. General theories of the regulating mechanisms involved in the control of species numbers have ranged from extrinsic factors such as changes in food (Lack, 1954; Pitelka *et al*., 1955), climate (Andrewartha and Birch, 1954), predators (Craighead and Craighead, 1956), parasites (Varley, 1947), and diseases (Bendell, 1955) to intrinsic changes in reproductive rates or endocrine activity (Christian, 1950). In recent years attention has been directed to the intrinsic or evolutionary changes in behaviour as a regulating mechanism (Carrick, 1963; Wynne-Edwards, 1962), and even to causes inherent in the genetic composition of species (Chitty, 1965; Wellington 1960; Krebs, 1964).

My hypothesis at the beginning of this study was that mostly extrinsic factors (food and climate) maintained bear populations at existing levels in different habitat types and accounted for some of the yearly fluctuations in numbers within a habitat type. This study was designed to test that hypothesis and associated problems by marking known-age animals in a natural habitat and checking their growth, survival, and interrelationships through recaptures and observations over an extended period, evaluating carefully the different components of their habitat, and relating each to the other.

Only in recent years has it been possible to conduct field studies on wild bears by capturing them repeatedly. Advances in handling large wild animals with drugs and projectile syringes have made this feasible. Studies of bears prior to 1957 were rather casual field observations or morphological studies; a great deal on the biology of bears had been written, however, based on general impressions and assumptions.

Most recent studies of the black bear have been centred in eastern North America in deciduous forests. King *et al.* (1960) worked on the pathology, parasitology, and hematology of the black bears in New York, and Wimsatt's (1963) study of delayed implantation in bears was also conducted in New York. Erickson (1957, 1959) and Erickson *et al.* (1964) undertook long term ecological and reproductive studies on black bears in northern Michigan. Their studies, which were concerned primarily with reproductive rates and the management of the species, have provided excellent data for comparative purposes on litter sizes, age at sexual maturity, ovarian function, and self-sufficiency of young. Stickley (1957, 1961) has done some recent research on black bear ecology in Virginia, and he has given estimates of reproductive rates and home ranges of black bears living in deciduous forests.

Little has been known of the biology of bears in the spruce (*Picea* spp.) forests of western North America. Rausch (1961) has published on black bears in Alaska and presented good growth and dentition data on wild and captive bears, in addition to notes on parasites, denning habits, and reproduction. Practically no work has been done on natural mortality or on behaviour in black bears, nor has a serious attempt been made to determine what forces regulate bear numbers. The management of black bears in many areas has been left either to persons with a special interest in its destruction, such as stockmen and lumbermen, or has merely followed general theories of game management. Current work on some of these problems is being conducted in Wisconsin, Washington, and Wyoming. Major works on other species of bears throughout the world have been largely based on opinion, general observations, or morphological studies (Couturier, 1954; Davis, 1964; Pederson, 1957; and others) and offer few comparative data. Studies of bear behaviour have been general or based largely on captive animals (Meyer-Holzapfel, 1957). The behaviour of the black bear has been particularly neglected.

Discovering information useful in the management of a game species usually is, of course, the ultimate purpose of research on that species, whether other research goals are met or not. I hope that this study has contributed both to better management of black bears as a game species and to a solution of biological problems basic to bears and all animals.

CHAPTER TWO

THE STUDY AREA

This study has been centred in the Big Creek drainage 10 miles north of Whitefish, Montana, on the eastern slope of the Whitefish Range of mountains (Figure 1). The drainage is approximately 80 square miles in area, and Big Creek flows in a northeasterly direction into the North Fork of the Flathead River, a south-flowing stream that parallels the Whitefish Range. Almost the entire drainage is Federally owned forest crop land. The main branches of the drainage are accessible to vehicular traffic along logging and fire control roads (Figure 2). Since this study area presents quite a different environment than does the habitat described in other studies of black bears (see Chapter 4), a description of the physical characteristics is essential.

Geology and Topography

The Whitefish Range is an uplift of Pre-Cambrian sedimentary rock associated with the Livingstone Mountains that form the Continental Divide, which is about 30 miles to the east in Glacier National Park. There are scattered basaltic intrusions throughout the drainage (Jonkel, 1959).

The area is dominated by numerous small valleys divided by sharp ridges. There are abrupt changes in elevation

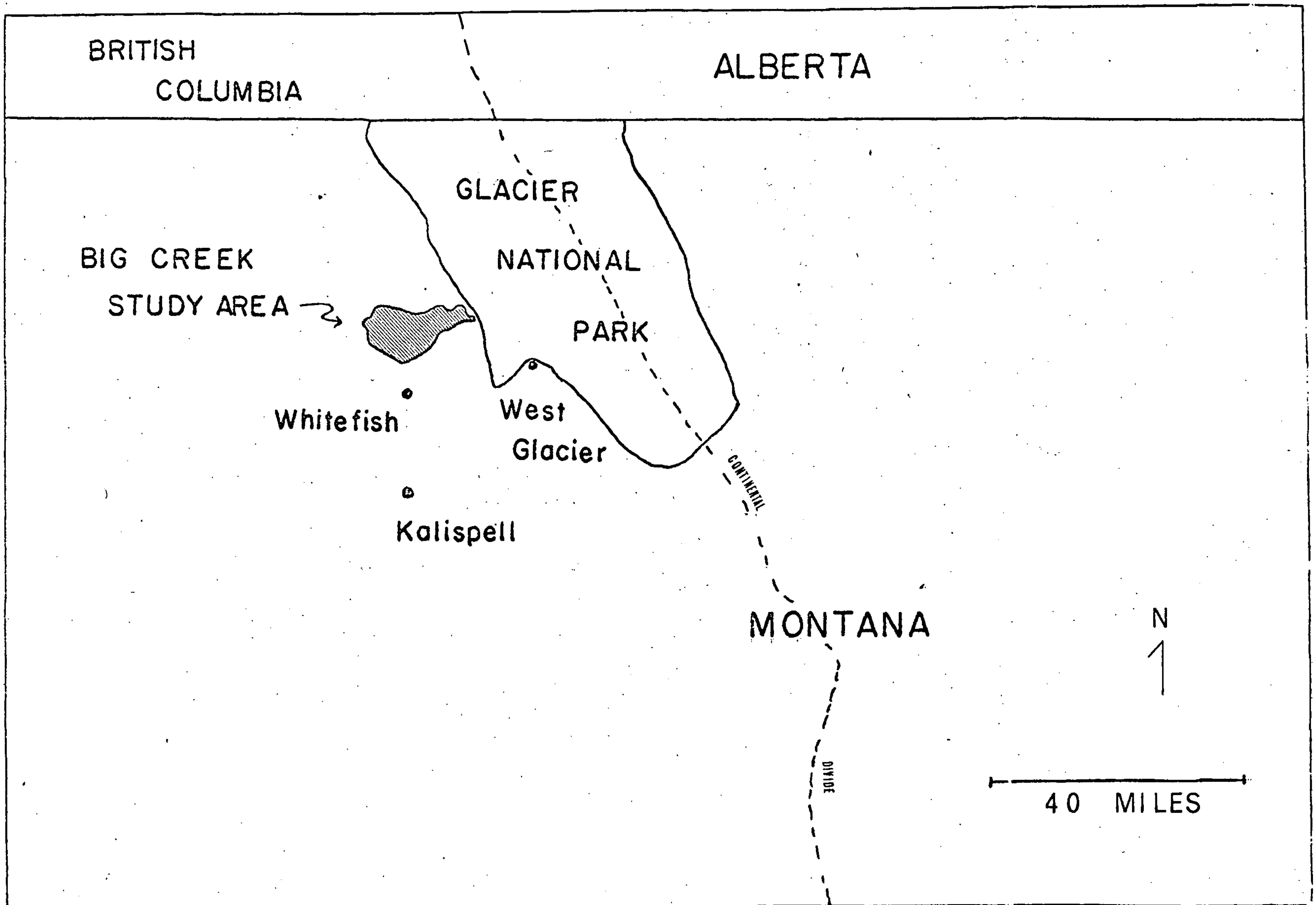

Figure 1. Geographic location of the Big Creek study area.

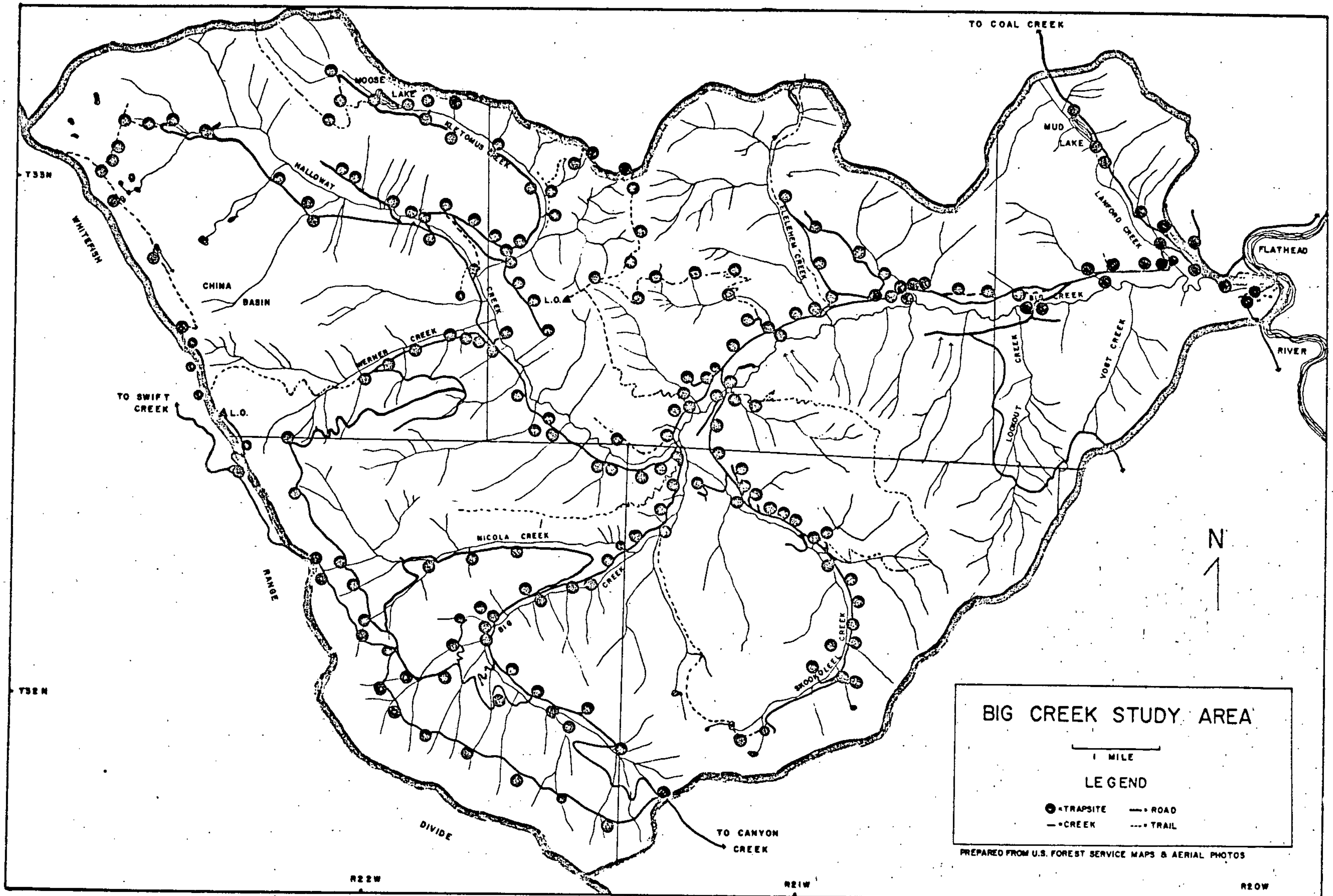

Figure 2. Detail of the Big Creek study area showing the location of roads, trapsites, drainages, and other pertinent data. Trapsites were restricted to roads and trails, but observations were made throughout the area.

from about 3,800 feet up to 7,521 feet at the highest point. The entire area is characterized by steep hillsides, cliffs, and narrow stream bottoms.

Climate

The climatic conditions vary considerably from the lower to the upper reaches of the study area and from one slope to another. Its upper portions lie close to the centre of a Pacific storm track, which causes the area to take on maritime aspects during winter and sometimes during fall or spring, and which results in snow depth up to 10 feet, while south slopes at lower levels often remain relatively snow-free. Precipitation comes mostly as snow, as shown in the annual and monthly precipitation averages for West Glacier, 14 miles southeast of the study area (Figures 3 and 4). The same weather patterns predominate at the West Glacier station as on the study area, and these data can be taken as representative of average conditions throughout the study area. Mean monthly temperatures range from around 20°F in winter to the low sixties in spring and summer. The temperature data for the West Glacier Station are also presented in Figure 4, but the topography of the Big Creek drainage renders all average climatic values of little local significance. Extremes of semiarid areas and rain-forest lie adjacent in many parts of Big Creek as a result of differences in aspect and slope.

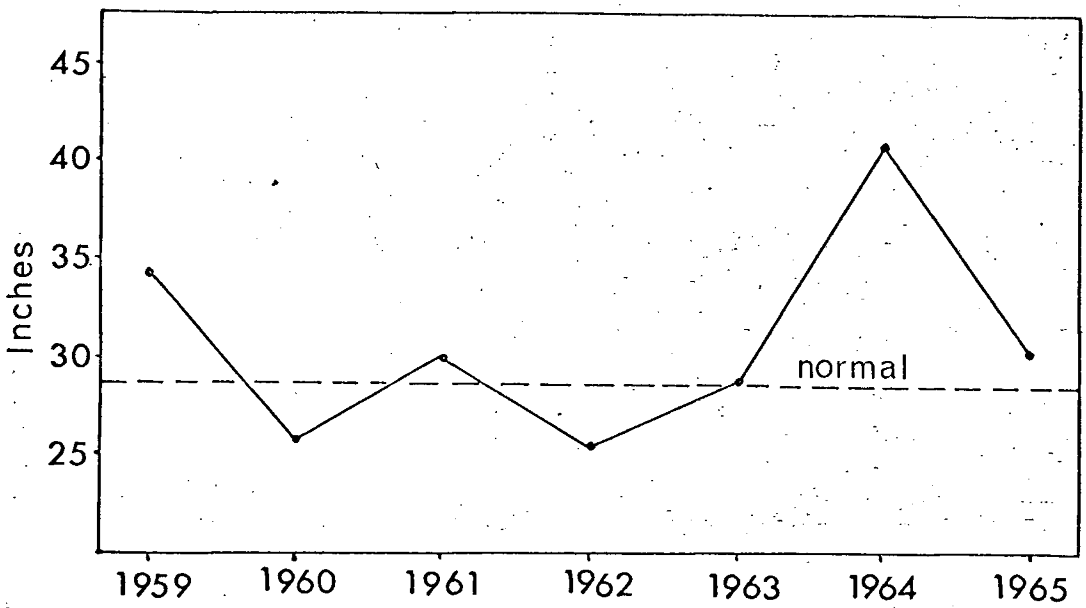

Figure 3. Annual precipitation at the West Glacier, Montana, station. Compiled from Annual Summaries, U. S. Weather Bureau 1959-1965.

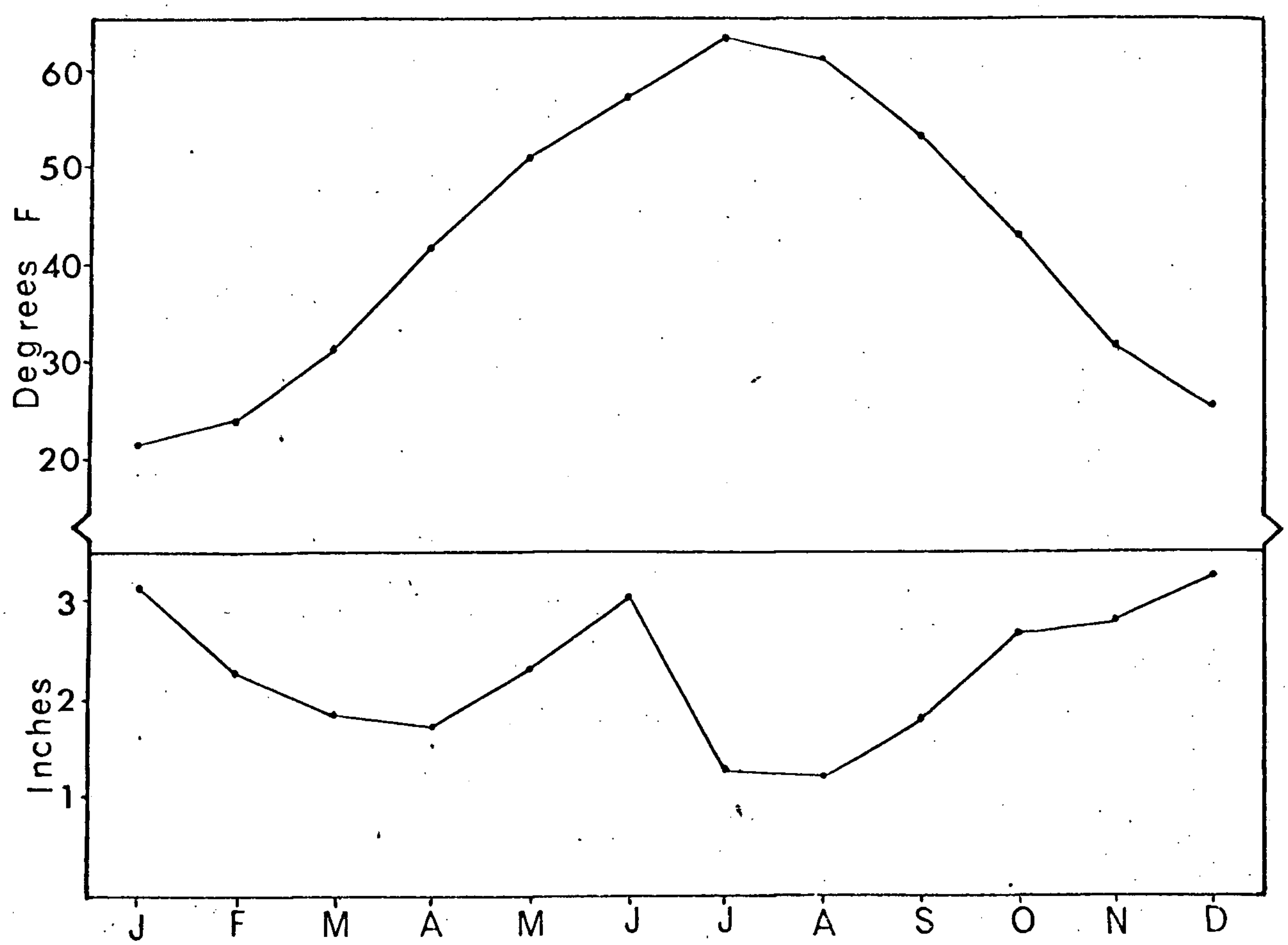

Figure 4. Average daily temperature and monthly precipitation at the West Glacier, Montana, station. Compiled from Annual Summaries, U. S. Weather Bureau 1959-1965.

Vegetation

Since the black bear is a forest animal and is primarily a vegetarian seeking its food from plant sources that change with the seasons, a botanical consideration of the study area was necessary. In the following description only plants or floral conditions of importance to this study are described.

By the classification of Daubenmire (1952), the Big Creek study area lies in the spruce (*Picea engelmanni*)-fir (*Abies lasiocarpa*) zone, although Douglas fir (*Pseudotsuga menziesii* var. *glauca*) and ponderosa pine (*Pinus ponderosa*), and western red cedar (*Thuja plicata*) tree unions (a group of trees and other plants with similar requirements) form local near-climax stands on some exposures. Alpine conditions exist on some of the highest peaks.

The Closed Forest. The main forest on the area is composed of a dense spruce-fir stand (Figure 25 in Appendix). Tisch (1961) has given an extensive account of the vegetational conditions on Big Creek, including a succinct description of the climax forest. This forest covers approximately 80 per cent of the drainage, and is divided almost equally between *Picea*-*Abies*/*Menziesia glabella* and *Picea*-*Abies*/*Pachistima myrsinites* associations.

Tisch also described the seral vegetation on the area, but he did not emphasize that a large part of the study area was burned at some time in the past (Figure 5). The seral stands comprise a major portion of the bear habitat and vary

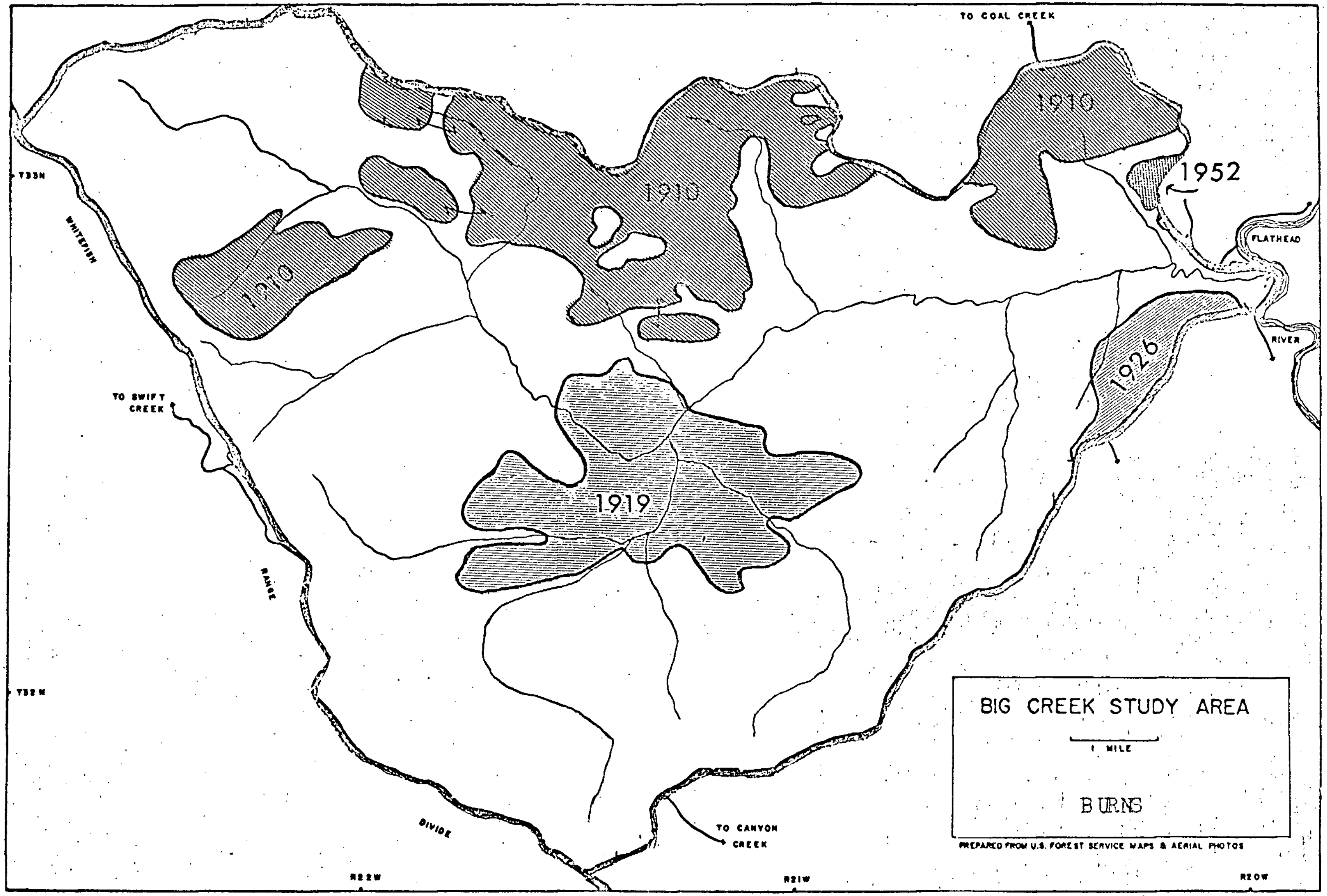

Figure 5. Portions of the Big Creek study area that have been burned since records were first begun on the area. These burns provide an additional diversity to the area by creating openings and seral stages of vegetation important to bears.

with age and site; they are very dense and are composed mainly of either larch (Larix occidentalis) or lodgepole pine (Pinus contorta), but all show an orderly succession towards the climax spruce-fir forest.

The Open Forest. The more open portions of the forest encompass about 10 per cent of the total area. They are found either at (1) the higher elevations where the spruce-fir zone is dominated by mixed stands of wind-deformed, widely spaced whitebark pine (Pinus albicaulis) and spruce among low-growing shrubs and forbs of the Picea-Abies/Menziesia glabella association, or (2) at low elevations on southerly facing slopes. The second type is composed of near-climax stands of either the Douglas fir or ponderosa pine unions, and is found under topographic conditions characterized by steep, rocky, southerly facing slopes (Figure 26 in Appendix). This second open type of forest has an understory dominated by vegetation from both the Picea-Abies/Pachistima myrsinites association and the various associations formed by Douglas fir. Daubenmire (1952, 1953) has made detailed descriptions of these vegetative types.

Open Areas. There are natural and man-made treeless areas on Big Creek, but they total less than 10 per cent of the entire drainage. The major open areas are near-alpine tundra and grassy parks on the highest peaks, talus slopes along north faces of the highest ridges and peaks and on southerly facing slopes at lower elevations, wet and dry mountain meadows, snowslide areas, creek bottoms, roadsides, and clear-cut logged areas. The vegetation of the wet and dry mountain meadows, the snowslide areas, creek bottoms, and roadsides is especially important to bears, as was shown in the food habits study by Tisch (1961). They should be described briefly for this study, since they were important in the observation of bears.

The wet meadows are generally small and are surrounded abruptly by mature spruce. The poor drainage evident in these areas may account for the absence of trees. Wet meadows often follow poorly developed drainage courses and may be quite extensive in long, narrow patterns. Sedges (<u>Carex</u> spp.) and Bluejoint grass (<u>Calamagrostis canadensis</u>) predominate in these meadows.

The dry meadow type makes up about one per cent of the total area, but is quite widespread in small patches on many of the southerly exposures and ridges at all elevations (Figures 26 and 28 in Appendix). Both exposure and soil factors seem to be involved in maintaining this type, as the soil is shallow and rocky, allowing good drainage as well as high evaporation rates under a direct sun. Dry meadows are usually dominated by the <u>Agropyron spicatum</u> union of Daubenmire (1953:304) and bordered by an open stand of Douglas fir. Common plant species are <u>Agropyron spicatum</u>, <u>Festuca idahoensis</u>, <u>Balsamorhiza saggitata</u>, <u>Achillea millefolium</u>, and <u>Carex geyeri</u>. The meadow often incorporates rocky outcrops and cliffs, patches of shrubs typical of Douglas fir associations, and single Douglas fir or Rocky Mountain juniper (<u>Juniperus scopulorum</u>) trees. Except for these incorporations, some of the dry meadows extend for several acres on the broader slopes, or may exist as narrow fingers along the crests of forested ridges.

Snowslide areas are common on the upper portions of the study area and are created and maintained by the annual movement of snow down traditional courses. They usually originate in dry meadow or cliff areas and extend to the valley bottom in narrow strips, cutting abrupt paths through the timber (Figure 27 in Appendix).

The wider streams in the drainage, through their flooding and meandering action, maintain openings in the forest canopy of the main valleys. These openings are generally dominated by shrubs such as alder (*Alnus* spp.) and redozier dogwood (*Cornus stolonifera*) and by large forbs such as *Heracleum lanatum*, *Angelica* spp., and *Equisetum* spp.

Open areas that have been created by man are the roads and clear-cuts (logged areas that were cleared of all vegetation and scarified). Both are subject to invasion by exotic species and by native plants that are lovers of disturbed areas.

Land-use Practices

Early in the nineteenth century bears and fur animals on the study area were trapped extensively by commercial trappers. From 1932 to 1939 sheep were pastured along the open divide country at the head of the drainage and along some of the major ridges. The bands were of about 2,000 head maximum and spent only part of the time within the boundaries of the study area. Apparently considerable numbers of bears, both black and grizzly, were shot during this period, but no records were kept of the actual numbers. No stock has been pastured in the area since.

The first roads were put into the area in 1933 and 1934, but little logging was done until the early 1950's. For the past 15 years it has been under intensive management by the United States Forest Service and many areas have been logged (Figure 6). A Forest Service camp is located at the extreme lower end of the study area.

Elk (*Cervus canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and whitetail deer (*O. virginianus*) are common and attract some hunters to the area; Spruce Grouse (*Canachites canadensis*) and Blue Grouse (*Dendragapus obscurus*) are also hunted for a short period in the fall.

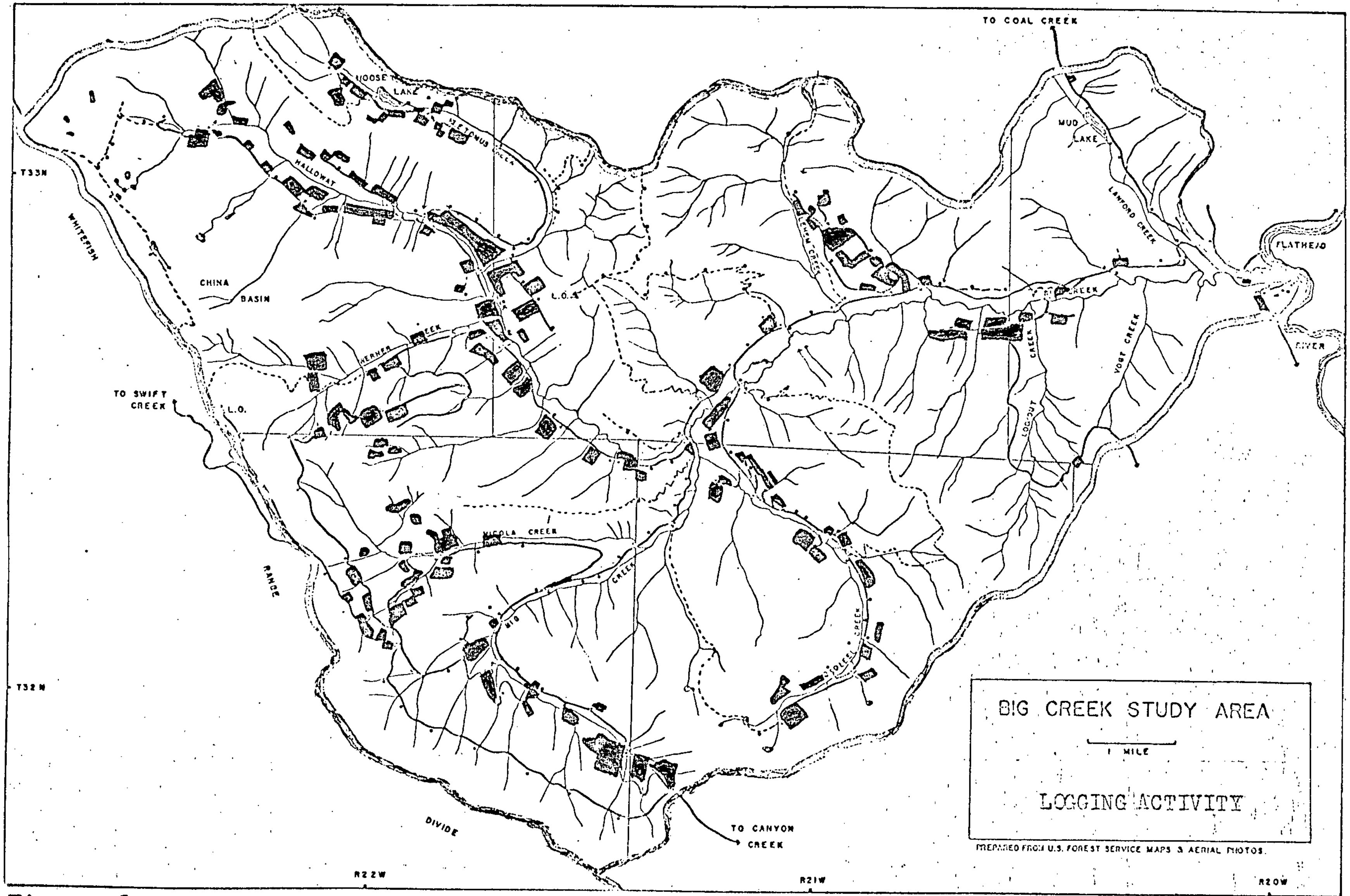

Figure 6. Logging activity on the Big Creek study area. The black areas have been clear-cut just before or during the study period.

CHAPTER THREE

METHODS

Studies were begun on a single drainage system surrounded completely by natural bear habitat in order that the study area could be expanded if necessary. The Big Creek area was chosen because (1) bear density was known to be high in the area; (2) there was a good system of roads and trails throughout the drainage; and (3) extensive open areas promised to be an aid in making observations of marked animals. Botanical collections and evaluations were made personally or in cooperation with Edward Tisch, a University of Montana graduate student. Maps of the area were prepared with the aid of United States Forest Service maps, aerial photos, and ground observations. Field studies were restricted primarily to May through September.

Bears were captured in modified Newhouse 150 steel traps (Figure 23 in Appendix) as first used by Black (1958), and trapping techniques followed his method and those of Erickson (1957). Traps were placed throughout the study area. Surrounding drainages were also trapped, but to a lesser extent. Traps were originally placed 0.5 miles apart along logging roads in the area, but this procedure was modified to fit local conditions as the study progressed. The most successful set was a cubby (Figure 22 in Appendix) built with logs and rocks against a hollowed bank, with the bait placed in the rear of the cubby, and the trap set at the entrance. Stepping sticks were placed around the trap and anchored securely. The movements of a bear just before capture could thereby be carefully controlled, insuring that the bear would be captured in the desired manner. Small mammals and birds were sometimes a nuisance in disrupting the sets or in tripping the traps. Their disturbance of sets contributed to the escape of bears that were improperly captured and to the injury of others through atypical captures. When the trap functioned properly, the bear was held transversely across the paw just above the main pad. Occasionally, especially with small bears, the trap closed too high on the leg, and some legs were broken in this manner. I found that these injuries could be reduced by keeping the trap jaws oiled so the trap closed as the foot was descending.

I used a similar set with the Aldrich snare trap (Figure 22 in Appendix) when trapping on trails some distance from roads. The snare trap was light in weight, but it was more difficult to set. Traps were either anchored fast or attached to a heavy drag. Both types of trap were efficient in capturing bears of any age.

Initial experiments with succinylcholine chloride (Sucostrin, Squibb Institute, New Brunswick, New Jersey) were made on captive wild bears from Yellowstone National Park to determine the dosages necessary to immobilize bears. The methods of Black *et al*. (1959) were followed; numerous adaptations were made in the technique, however. Dosages were calculated from the estimated weight of each captured bear, and the drug was administered intramuscularly with the aid of an automatic projectile syringe fired by a carbon dioxide powered long range syringe projector ("Cap-Chur" gun, Palmer Chemical Company, Inc., Atlanta, Georgia). Occasionally the drug was administered manually by the use of a hand hypodermic syringe or else a hand syringe mounted on the end of an aluminum pipe. Supplemental dosages were given with a hand syringe.

Succinylcholine chloride administered on the basis of 1 mg per 2.3 kg of estimated body weight approximated an ideal dosage for most animals, but was excessive for a few. Bears were easily saved from lethal dosages by administration of artificial respiration until the excess drug hydrolyzed. Bears were kept immobilized to three hours with small supplemental dosages of 5 to 10 mg, but normally an animal had fully recovered from the initial dosage within 30 minutes. No deleterious side effects of the drug were noted. Bears were generally sufficiently immobilized from approximately five minutes after administration of the drug until about 20 minutes later. Some individual and seasonal variation in the response to the drug was noted; bears in the autumn remained immobilized almost twice as long as the thinner bears given comparable dosages in the spring. This agrees with the findings of Craighead *et al*. (1960) on grizzly bears, but Stickley (1961) found no marked differences in the response of thin and fat bears. Complete familiarity with the action of the drug proved as valuable as the drug itself.

During February, 1960, three denned bears were given dosages of succinylcholine chloride. Since the bears were in a semidormant state with an apparently reduced metabolic rate, it seemed logical that susceptibility to the drug might be higher. Smaller dosages were unnecessary, however, as the bears were not immobilized until given normal dosages of approximately 1 mg per 2.3 kg of body weight.

All animals were marked in several ways. Metal stock tags that varied by number and colour were placed in both ears of every bear. A distinguishing number was tattooed in the tip of each ear or beneath the right foreleg of some animals. Vinyl tape ribbons (Craighead and Stockstad, 1960) were placed in slits in the ears, separately from the tags, and riveted. The location in the ear of both the tags and the ribbons was varied for different animals to give additional individual colour combinations. The metal tags were more durable than the ribbons, and except for some initial losses they were permanent throughout the seven years of the study. Ribbon loss was greater, especially from breaks close to the ear. Because of fading, all ribbon colours became difficult to distinguish after two or three years. Even so, many bears were identified by the plastic ribbons five years after they had been placed in the bears' ears. The artificial markers caused some indignation among people who frequented the area, and some biological information was lost when resentful hunters failed to report kills, even though I tried to counter this problem with talks and press releases. Natural markings were used in combination with these artificial methods.

All bears were weighed with spring scales. Cubs were weighed while in the trap or were weighed by hooking a foot onto the scale. Larger bears were rolled onto a square canvas; the corners were hooked onto the scale, and both bear and canvas were lifted manually or with the aid of a pole tripod and block and tackle.

The bears were guarded against injury as much as possible. Traps were checked twice a day and sometimes more often in order that the animals captured would not spend too long in the trap; all bears with cuts or other wounds were treated with a strong antiseptic, and some were given an intramuscular injection of antibiotic (penicillin and streptomycin). Only one out of every 20 bears received a serious wound from the trap. At least one member of the trapping crew remained with recovering animals until they were able to stand and begin to move away. Immobilized bears were covered with a tarp during bad weather.

Observations of bears were made with the aid of 6 x 30 power field glasses and a 30 power spotting scope. During the mornings and evenings open hillsides were scanned or watched with field glasses, but identifications were usually made with the spotting scope. Observations made by loggers and Forest Service personnel were also evaluated and recorded.

Observations in drainages surrounding the study area were made systematically, and the numbers of tagged and untagged bears were recorded to measure dispersal. With the cooperation of United States Forest Service and Montana Fish and Game Department personnel, observations of the adult to young ratios throughout the bear range in Montana were recorded. Hunters in the vicinity of the study area were asked about bear kills, and the ratio of tagged to untagged bears killed was recorded for use in calculating population density and for management.

Sample transects were established to compare available foods with foods consumed by bears. Four permanent huckleberry (*Vaccinium* spp.) transects were established at the 5,000 foot level, with each transect at a different exposure. Another transect was placed at 5,800 feet with a southern exposure, and another, at the 6,600 feet, again with a southern exposure. The relative abundance of berries at all levels was recorded each year. A four mile transect was established in the whitebark pine forest with trees sampled for cones at 100 pace intervals. Ten selected whitebark pine trees were also permanently marked with metal discs so that individual trees could be compared. Each September the total number of cones on all trees was counted with the aid of the spotting scope.

I examined bears for parasites whenever time permitted, noting the species and abundance of each, and all dead bears were checked for internal parasites.

Phenological data were recorded to evaluate annual climatic differences in relation to bear activity. Information on the movement of individual bears was obtained, and den sites were located by tracking bears in the snow. Other dens were found by contacting hunters and loggers and by soliciting information through the press. Dens were observed periodically during the winter and again in May to determine winter mortality rates.

Skeletal material was cleaned with dermestid beetles and stored. Tissues, reproductive tracts, etc. were placed in 10 per cent formalin. Ovaries were hand sectioned with a razor blade at approximately 2 mm intervals to make corpora lutea counts, and teeth were decalcified and sectioned as described by Stoneberg and Jonkel (1966) to determine age. Some female reproductive tracts were obtained from the Washington Game Department for comparative studies.

Indications were that too few black bears were being killed by hunters to effect good management of the species as a game animal. Therefore, I tested a management technique to determine whether bears would come to roads where they could be hunted more easily. In the fall of 1960 I seeded one-tenth mile strips of roadbed to white clover (*Trifolium repens*) and orchard grass (*Dactylis glomerata*) at every mile along 16 miles of the Big Creek road. The plantings ranged from about 4,000 feet to 6,000 feet. The seed was spread with hand rotary seeders directly onto snow or onto wet ground soon covered with snow. Since 1962, periodic observations have been made along this 16 mile area, and the numbers of bears on the strips and the numbers of bears off the strips have been recorded.

The reproductive condition of females was determined by examinations of the vulva. The degree of swelling was ranked on a scale of zero to four based on measurements and colour. Animals ranked at stages three and four were considered at the peak of the estrous cycle.

The methods used in studying wild populations are important for several reasons. Capturing and handling procedures can increase mortality or can induce some species to change their habits; they may flee from the area, or cease using certain parts of their range. Also, if a species is rare, is valuable esthetically, or is prized as a trophy, the composite value of the research can be negated through unnecessarily deforming or defacing individuals of the population. Obviously, the less that research procedures upset natural conditions the better that particular research will be. I have tried to follow these precepts. Many bears became accustomed to being captured and would sit quietly even when I approached, but bears that were injured usually became frightened. This fear of the trap and of man usually was evident in future captures and probably made some bears trap-shy, though I do not believe this disturbance became significant during this study.

PART II

RESULTS:

CHAPTER FOUR

ECOLOGICAL STUDIES

The study of the population dynamics and management of a species must be based on ecological information from natural populations. This involves the development of special techniques and a careful selection of the study area. Lack (1965) has pointed out that it is already becoming difficult to study animals in the conditions under which they evolved, and that without those conditions our studies are irrelevant to an understanding of the evolutionary aspects of ecology. Functional ecology, the study of the distribution and abundance of animals irrespective of evolutionary considerations (Andrewartha and Birch, 1954), is equally important. I wanted an area in which to study the functional problems, such as what environmental forces are important to bears and what changes in the environment affect bear populations. At the same time, I wanted an area in which to study the evolutionary adaptations of a population living under natural or nearly natural conditions. The forests of Big Creek, ranging from completely undisturbed areas to completely transformed areas, the annually increased disturbance of the forest in portions of the drainage by man, and the great variety of plant associations found within short distances led me to consider Big Creek such an area.

Home Ranges of Bears

Big Creek is divided into two basic types of habitat: one meets all the needs of individual animals and is inhabited year-round by bears; the other provides supplemental food and cover and has seasonal use from mid-July through autumn.

On the basis of 280 captures of 158 bears and 312 observations, I determined that most of the bears, both males and females, were confined to a certain part of the year-round habitat. As shown in Figures 7 and 8, both male and female adults tended to be captured or observed repeatedly in particular areas, even though trapping operations or observations were equally intensive throughout the study area. The area in which each bear was regularly captured or observed from year to year was considered that bear's home range. The extent of their home ranges did not change much with additional captures and observations or with time. Bears No. 19 and 62 illustrate this pattern most clearly. Bear No. 19, a female, was captured or observed 15 times (four captures, 11 observations) between July 25, 1959, and June 2, 1965. She was never seen or caught outside an area on upper Hallowat Creek that measures 2.0 miles in maximum length (see Figures 2 and 7). Bear No. 62 (Figure 8), an adult male whose range extends from Points A and B, was captured or observed 17 times (six captures, 11 observations) between June 19, 1960, and May 22, 1966. He was never seen or caught outside of an area on Hallowat Creek that measures 6.0 miles in greatest distance between sites. The entire drainage is typified by locally abundant food,

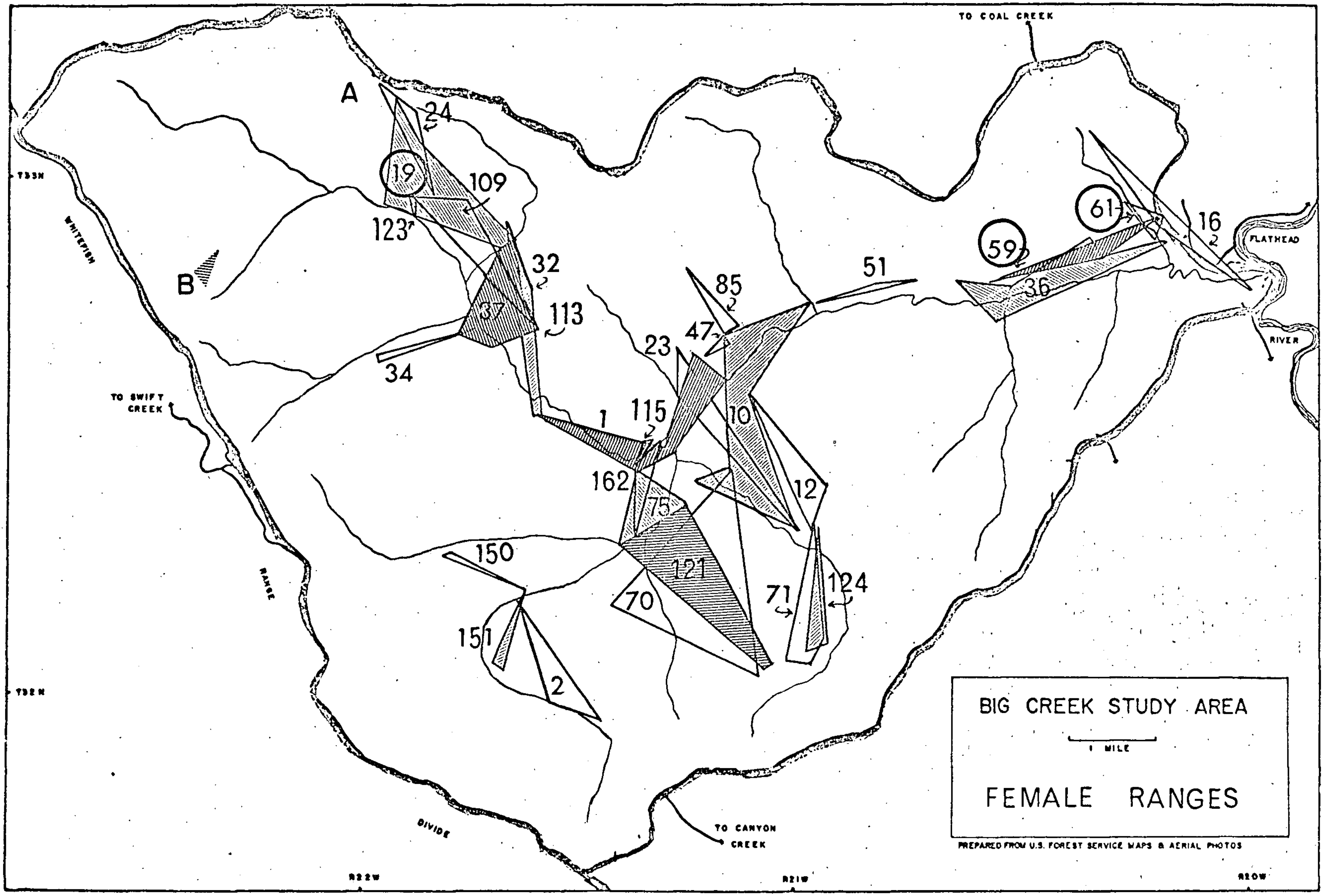

Figure 7. Minimum home ranges of adult females on the Big Creek study area based on capture and observation points. Only the ranges of bears discussed in the text are circled. Areas A and B are at approximately 6,000 feet in elevation and are typical of the habitat used seasonally by bears.

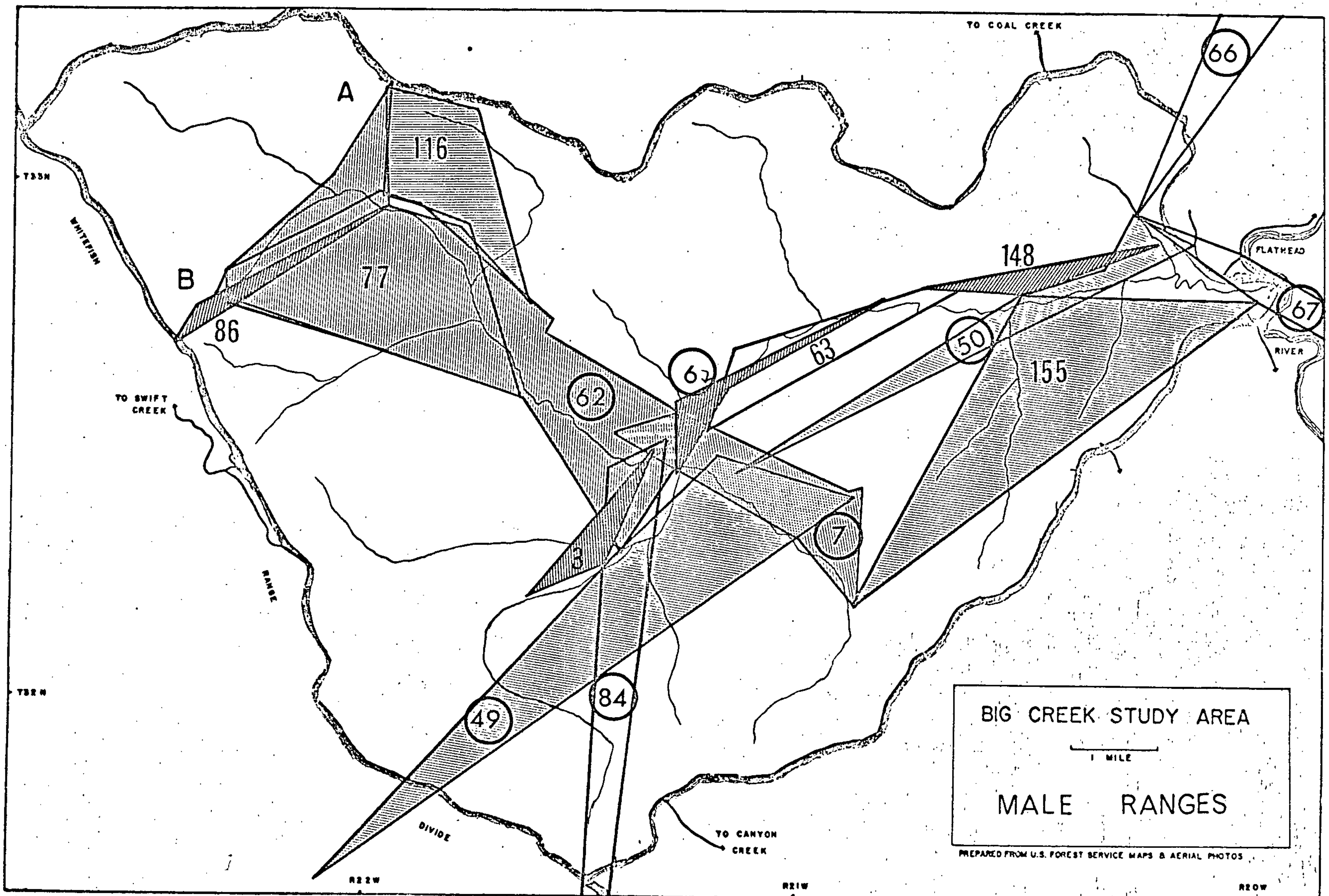

Figure 8. Minimum home ranges of adult males on the Big Creek study area based on capture and observation points. Only the ranges of bears discussed in the text are circled.

since the berry crop fails or is abundant at different elevations and on the various exposures each year. Only bears resident where the food was abundant made use of it, however; other bears did not congregate in that area. In addition, only a small part of those bears living one mile or more from the Big Creek Ranger Station, where food was abundant at the garbage dump, traveled to this food source. Other bears living close to the dump were regular visitors.

Bears adjacent to a seasonally used area such as Moose Lake (area A in Figures 7 and 8) or China Basin (area B in Figures 7 and 8) moved to these areas freely when food was available there. These two areas are at about 6,000 feet, and usually become clear of snow by early July. In Septembers of some years these areas have a great abundance of either huckleberries or whitebark pine cones. Bears do congregate in these places, and when feeding in such an area, they seem quite tolerant of other bears, approaching to within 100 or 200 yards of one another. Even so, individuals generally stay in one small part of the area. Eleven different bears were observed feeding on huckleberries in China Basin from September 6 to 15, 1961. Their movements are shown in Figure 9. There were four tagged adult male bears, an unmarked female and cub, and five large unmarked bears which seemed by their size to be adult males. The female and her cub and the one tagged sub-adult male (No. 129) stayed near the periphery of the huckleberry area, though berries were most abundant in the long central area shown in Figure 9.

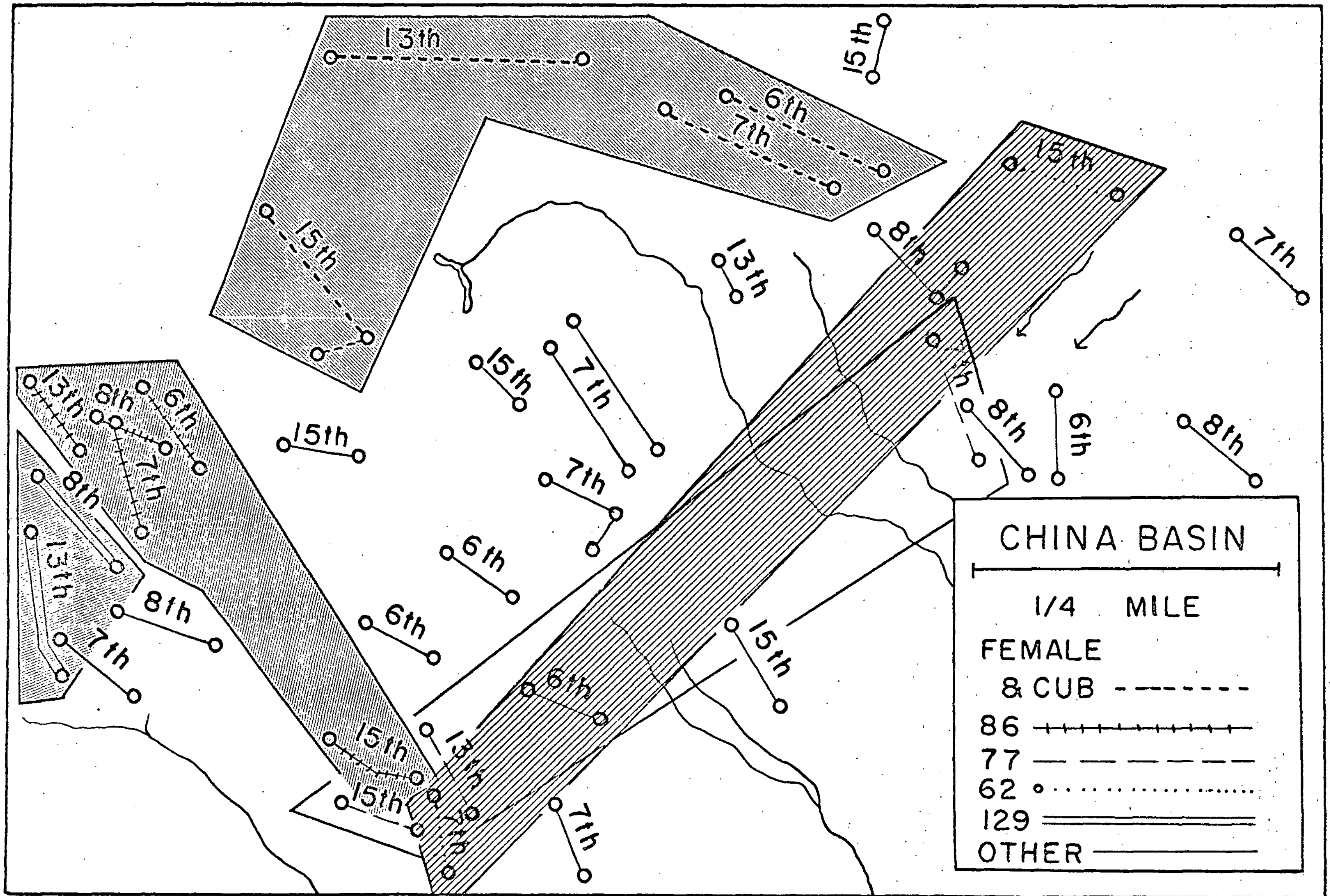

Figure 9. The movements of 11 bears observed from September 6 to 15, 1961, in the China Basin area of the Big Creek drainage. Shaded areas indicate ranges of bears observed most often.

The maximum distance between capture and observation points was measured for all adult bears on Big Creek. The results of 146 locations for 31 adult females and 83 locations for 16 adult males are shown in Table 1. A few adult bears made unusually long movements. Males No. 66, 67, and 84 (Figure 8) and females No. 125 and 156 (Figure 10) are examples. Female No. 156 and male No. 67 were animals with garbage dump experience that moved regularly between the Ranger Station dump and the village of Apgar 10 miles to the southeast. I have no information about the cause of the distant wandering of the other adults.

A comparison of Figures 7 and 8 shows that the ranges of the adult males and adult females overlapped, but there was a minimal overlap between adults of the same sex. Sub-adult ranges, though, overlapped considerably with adult home ranges. Trapsite 62B on lower Big Creek (Figure 2) was the site of the capture of two adult females during 1960, but seven different sub-adults were also captured at that site during the same period. Some of the sub-adults appeared to be transients, but others had home ranges almost identical to those of the adult females. Female No. 61 remained on the home range of her mother (No. 59) at least through 1965 when she was 5-1/2 years old (Figure 7). I noted six other cases of entire litters staying on their mothers' home ranges after the family groups had broken up. Additional data on this topic are in the Chapter on behaviour.

Bear No.	No. of Years Involved	No. of Points	Distance in Miles	Bear No.	No. of Years Involved	No. of Points	Distance in Miles
Females				Males			
1	2	6	2.1	3	4	4	2.1
2	3	6	1.7	6	3	7	3.0
10	6	12	2.5	7	7	7	3.4
12	7	5	1.6	21	1	2	2.0
16	2	3	2.5	49	6	5	7.4
19	6	15	2.0	50	6	6	5.7
23	6	4	2.5	57	1	2	4.2
24	4	3	1.5	62	7	17	6.0
32	5	5	2.2	63	6	4	3.3
34	2	2	1.2	64	3	2	6.3
36	2	5	2.4	77	3	6	3.6
47	4	3	.4	86	4	4	3.0
51	5	4	1.2	116	6	8	3.0
52	3	3	2.3	148	4	4	2.7
59	5	3	2.1	155	3	3	5.6
61	6	6	.5	167	2	2	.5
70	4	3	2.4				
71	6	10	1.7				
75	3	5	1.4				
85	4	3	.9				
87	6	6	1.3				
113	5	3	1.0				
115	2	4	.3				
121	5	7	2.2				
123	5	3	.3				
124	6	6	1.3				
150	1	2	1.0				
151	3	2	.9				
162	3	3	1.2				
177	1	2	.5				
192	2	2	.0				
Average			1.6	Average			3.9

Table 1. The maximum distance in miles between points of capture or observation for adult bears on the Big Creek study area during 1959 through 1966.

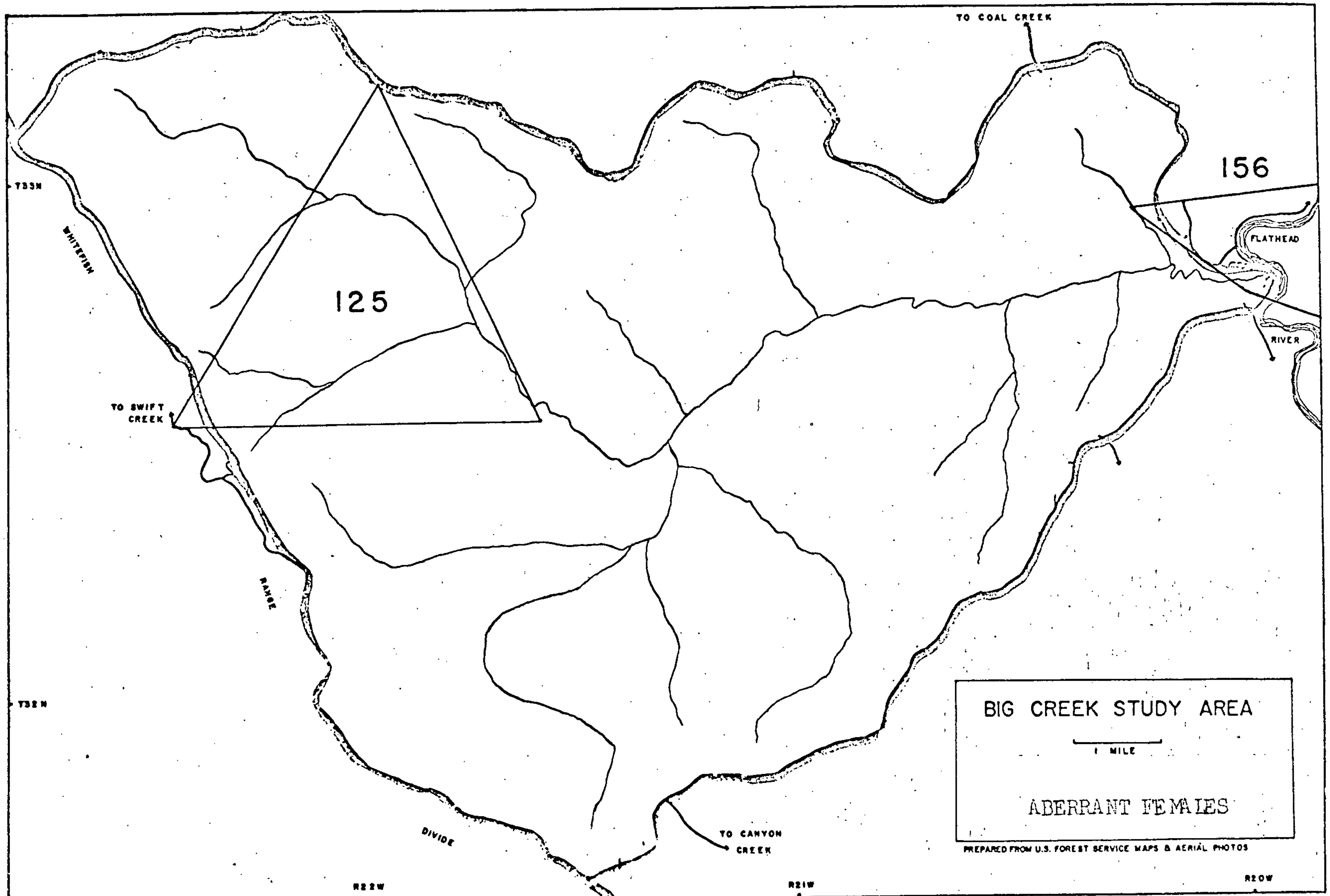

Figure 10. The movements of two aberrant adult females captured on the Big Creek study area.

The home range of some animals increased in size as the animal matured. For example, bear No. 7 (Figure 8), a sub-adult male when first captured in 1959, was captured and observed only in a small part of upper Skookoleel Creek through 1961. From 1962 (when he was a minimum of 6-1/2 years old) through 1965 he was captured or seen in that location and a lower area near the confluence of Skookoleel and Big Creeks. A large male, No. 6, was shot by a hunter in the latter location in 1961; apparently his death left that area open to bear No. 7.

Further evidence that the adult bears resident on the study area seldom leave their home ranges was provided by systematic observations in drainages surrounding the Big Creek drainage. Between 1959 and 1965 a total of 89 bears was observed in these surrounding areas. Eighty-five of these were untagged, and the remaining four were not seen clearly enough to determine whether they were marked. In many cases these "outside" observations of unmarked bears were made only a few horizontal miles from the home ranges of tagged bears in the Big Creek drainage.

Requirements of Home Ranges. Figure 11 shows the type of habitat in which 708 bears were either captured or observed between June 12, 1959, and May 30, 1966. Some data from areas adjacent to the Big Creek study area are included. There is some bias in these data since bears were most easily observed in open areas like the dry meadow type, and even the captures have some bias since I often trapped in the *Picea-*

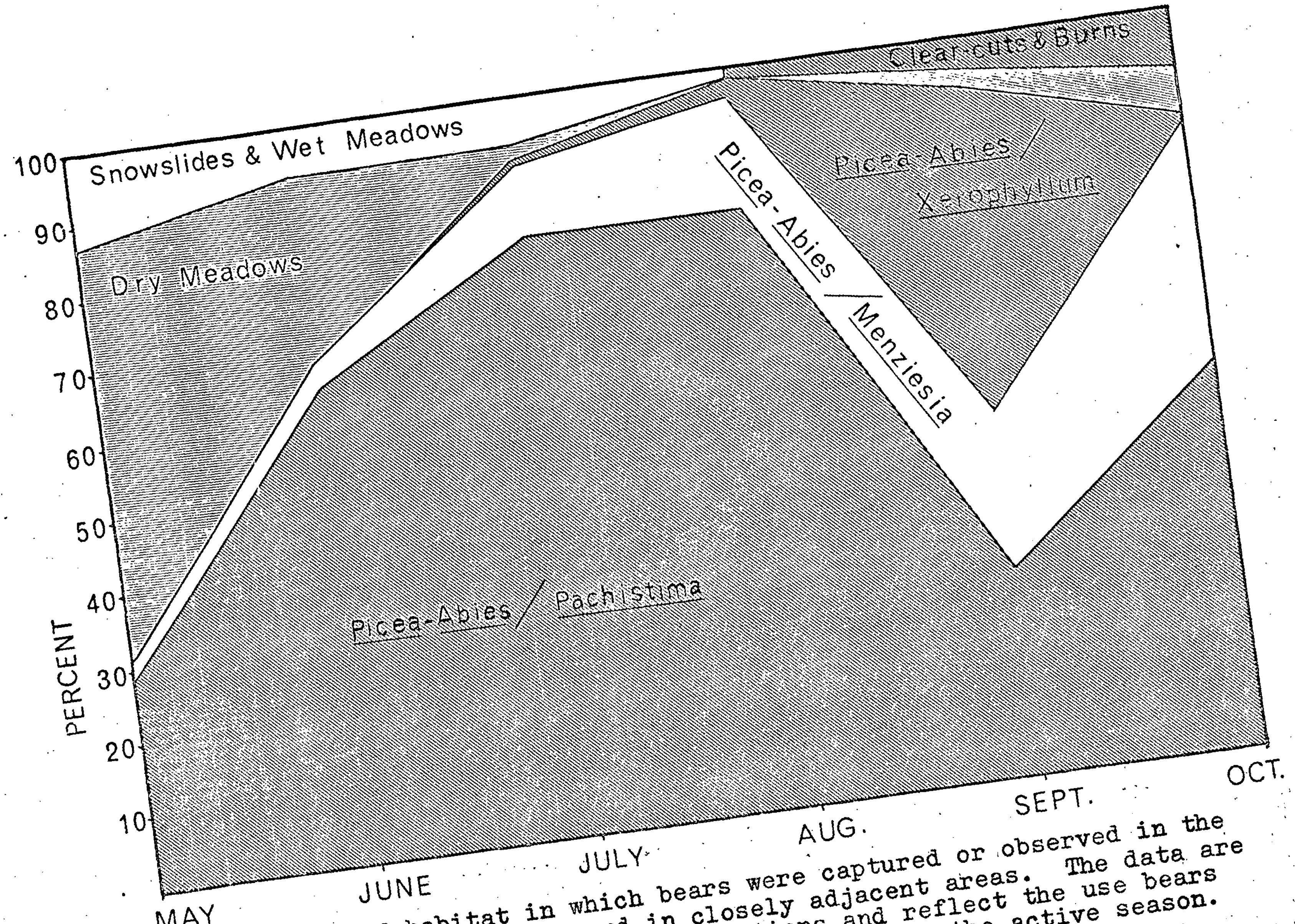

Figure 11. Types of habitat in which bears were captured or observed in the Big Creek study area and in closely adjacent areas. The data are based on 708 captures or observations and reflect the use bears make of different plant associations through the active season.

Abies/Pachistima association for specific bears.

As shown in Figure 5, much of the lower portion of the study area occupied by the Picea-Abies/Pachistima association has been burned in the past. These burns are now in various seral stages. All seral stages seem to be equally popular with the bears, but their neglect of clear-cuts in the Picea-Abies/Pachistima association indicates that they probably would not use recent burns even in that type. Recently logged areas in all types were almost completely avoided by the bears. New clear-cuts are being made in the area at a rate of up to one-half square mile per year.

Bears begin to use the clear-cuts as the seral vegetation becomes more dense. A cut area on Werner Creek (Figure 2) that was 10 years old in 1963 was used as much as the surrounding areas, since frequent captures and observations were made within the clearing. None of the seven bears observed in other cleared areas was feeding; apparently they were merely moving through the opening. The bears observed in cut areas were generally quite near the timbered edges, although in the dry meadow type they did feed up to one-quarter mile from the nearest trees.

Because the topography and habitat are so diverse on the area, no density or home range measurements were made within particular vegetative types. The only extensive climax forest left on the area is the Picea-Abies/Menziesia type. As shown in the description of the area, approximately two-fifths of the drainage is of this type, but only eight per cent of the captures and observations were made in it. In elevation the _Picea-Abies/Menziesia_ climax forest lies roughly between 5,000 and 6,000 feet, but extends lower on north slopes and higher on south slopes. This forest type clears of snow slowly, and so is avoided by bears until late in the summer. Also, as pointed out by Tisch (1961), it is poor in plant species. The understory often is composed completely of _Menziesia glabella_, and offers little food to any animal. In comparison, the dry meadow type comprises about one per cent of the area, but accounted for 55 per cent of the observations during May.

Movements Within Home Range Boundaries. Bears move to certain areas within their home range boundaries for various reasons, and this may group several animals. In the sections on bear density and habitat requirements, I have shown that small numbers of bears congregate to feed on dry meadow areas and on snowslides in the spring. They were always residents of the vicinity in which they were feeding, however.

Adult males seem to have more of a seasonal shift within their home ranges than do the females. In 1959, the first year of the study, the trapping project did not begin until mid-summer. Most of the trapping was done along the main roads at the lower end of the study area in the _Picea-Abies/Pachistima_ type. Of 16 adults captured that season, only three were males, which is significantly different from an even sex ratio at the five per cent level of the Chi-square

Test. In the following years, when the area had been trapped more thoroughly at all elevations, the sex ratio of adults was almost even (46.9 per cent females), indicating that the males were not in the permanent bear habitat with the females during late summer and fall of 1959. This hypothesis was confirmed by later observations, as, for instance, by the preponderance of adult males in the sub-alpine China Basin area during the autumn.

Bears also moved within their home range areas to the one-tenth mile strips I seeded along the Big Creek road in 1960. The plantings were slow in starting, probably because of the seeding methods and poor soil quality, but by 1962 the strips at the lower elevations were showing good growth (Figure 29 in Appendix). By 1964 even the strips at elevations near 6,000 feet were easily recognizable. Starting in 1962, I recorded whether bears observed along the 16 mile stretch of road were feeding on the seeded strips. Through 1966, 24 bears were observed feeding along the experimental road area; 14 of the bears were on the seeded portion, and 10 were outside it. Since the seeded strips comprise only 10 per cent of the total road-bed, this represents a thirteenfold increase in use of the seeded areas over the non-seeded areas. No tagged bears moved outside their home range areas to these seeded strips.

Den Ecology

On Big Creek a few bears emerge from their dens as early as mid-April, but, as shown in Table 2, most do not appear until mid-May. In some years, such as 1960, the snow melts earlier, and the dry meadow areas have green sedges and grasses by early May. In 1960 many bears were observed by the first week of May, and trapping operations were started on May 15th. The bears generally entered their dens by late October, but the fall of 1960 was unusual also in that the weather continued to be warm until the first week of November. There were no heavy frosts or snow, and food was abundant later than usual. Mountain ash berries (*Sorbus scopulina* and *S. sitchensis*), which do not usually ripen before they freeze or before the bears go to their dens, did ripen that fall and were eaten in great quantities (Jonkel, 1960). Much bear activity was noted, and trapping operations were successful until a snow storm came on November 8. In other years bears were usually denned by then; in 1961, for example, with the advent of heavy snows all activity had ceased by October 20.

A common belief is that bears in poor condition den for shorter periods than bears in good condition (Rausch, 1961; Spencer, 1955). Therefore, one might expect bears in poor condition to emerge earlier from their dens. On the Big Creek study area 60 per cent of 127 bears observed or captured during April and May were adults. Since adults are generally in better condition than sub-adults, the opposite

Year	Approx. date of first Emergence	Approx. date of General Emergence	Approx. date of Denning
1959	?*	June 1 ?	October 31
1960	April 10	May 5	November 7
1961	April 20	May 20	October 20
1962	April 20	May 15	October 31
1963	April 20	May 15	?
1964	?	May 25	?
1965	?	May 15	?
1966	?	May 15	---

*At points of question mark I was unable to be on the study area to get the necessary data.

Table 2. The approximate dates that bears entered and emerged from their dens on the Big Creek Study area. General emergence was arbitrarily taken to occur when bears comprising roughly 50 per cent of the population were seen throughout the snow-free portion of the drainage.

might have been expected, especially since adults comprised only 31 per cent of 155 bears tagged between 1959 and 1966.

The base of a hollow tree was the site most often used. Twenty-nine dens were located on the study area or within 100 miles of it, and 55 per cent of these were in hollow trees. Three were under fallen logs, five were in rock caves, one was under a cabin, and four were underground dens dug or enlarged by bears.

All bears made a hollow in which to lie, but only 10 out of 31 bears moved nest materials into the den. Erickson (1964) suggested that only females add nest materials to the den, but he thought this was because males den later in the fall when nest materials are unavailable. Three of 10 bears that moved nest materials into the den in this study were adult females; the sex of the others was unknown. One female stripped a great quantity of cedar bark from trees surrounding the den and made a large nest with this material. Two bears blocked the den entrance with nest materials in a manner similar to that of true hibernators.

A few bears modified their dens during the winter by adjusting the nest materials. Their activities during the denning period are discussed in greater detail in the section on behaviour.

Dispersal

During this study 18 bears were known to have travelled outside the study area. The greatest distance was a 30 mile dispersal by a 2-1/2 year old male. This bear was seen several times in mid-September as he moved south across the Flathead Valley, and he was finally shot on the outskirts of Kalispell. Four of the 18 bears were females, and three of these were 1-1/2 or 2-1/2 years old. The fourth female was an adult that was a dump addict (No. 156); she is discussed in the section on home ranges along with one of the adult males (No. 67). Three others of the 18 were adult males, but all of their movements from the study area were short enough (eight miles or less) that they might have been normal movements within part of their own range (Table 1). Five out of 10 sub-adult males that moved from the area were 1-1/2 or 2-1/2 years of age; the other five were first tagged as sub-adults, but their exact age was not known. The dispersal movements of the 10 sub-adult males and the three sub-adult females are presented in Figure 12.

Relative Distribution of Grizzly and Black Bears on Big Creek

Grizzly bears and black bears are sympatric on the Big Creek study area, but black bears are far more numerous. Since they are closely related species, some information on grizzlies was essential. Using capture and observation data, I estimated the entire grizzly population frequenting the area in 1961 to be six. It has not been as high since, although approximately that many grizzlies visit the area at some time each year. The black bear population was approximately 90 in 1961 (page 100), a ratio of 15 to one in favour of the black bears.

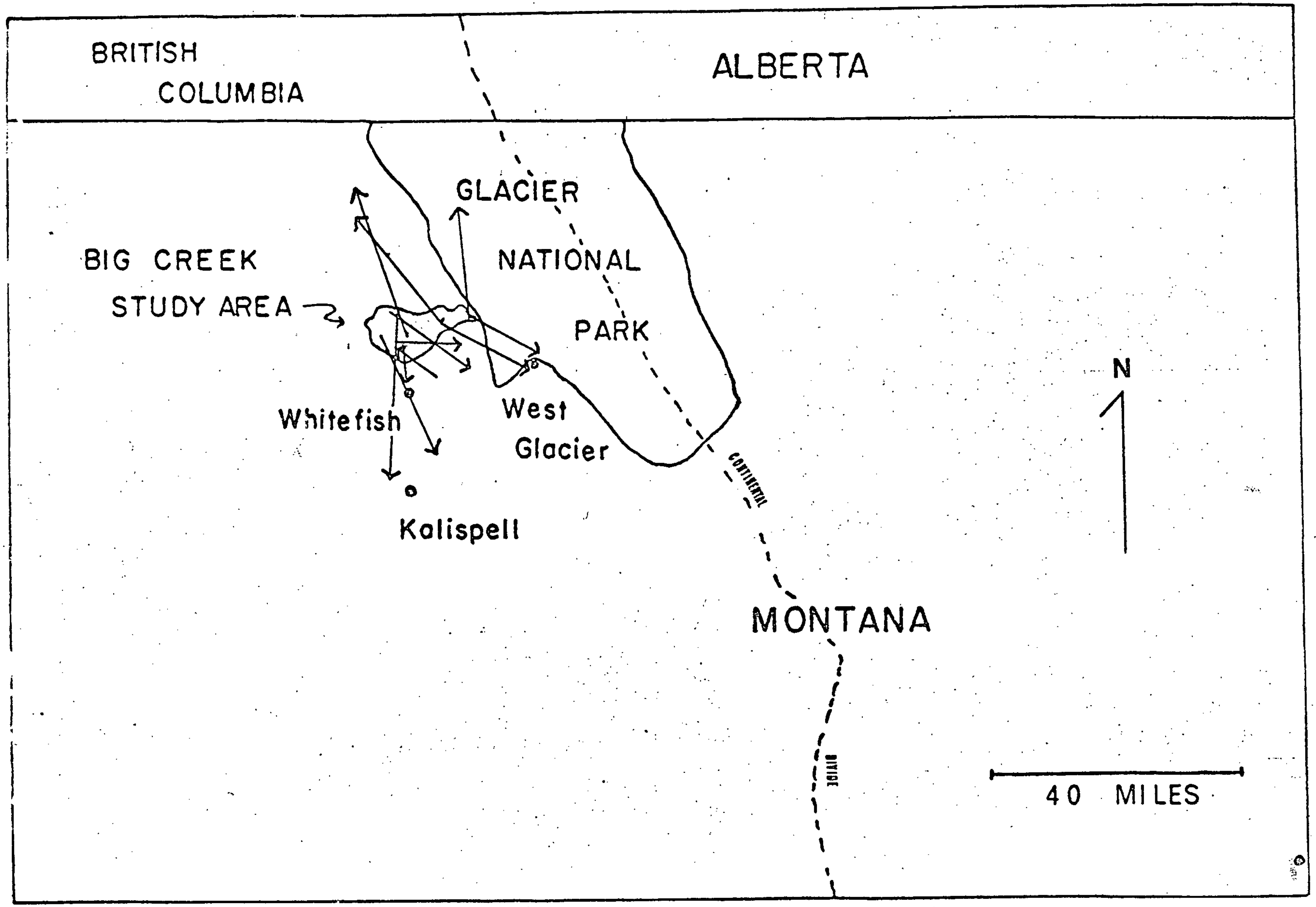

Figure 12. Dispersal of sub-adult bears from the Big Creek study area.

All captures and observations of grizzly bears were in typical black bear habitat. During early spring the grizzlies were mainly in the *Picea-Abies/Pachistima myrsinites* association with the black bears, but observations of tracks and scats and bear observations by loggers and Forest Service personnel indicated that grizzly activity was concentrated in the higher country in summer and fall. Repeated captures and observations of four grizzlies show that in the spruce-fir forest their home ranges are not much larger than male black bear home ranges, which concurs with the findings of Mundy (1963).

About 30 miles farther north in the Whitefish Range much of the timber has been burned repeatedly by large forest fires during the past 30 to 40 years. Treeless areas are much more extensive there, extending in many places for several miles. Climatic and topographic features otherwise closely resemble Big Creek conditions. Limited observations of bears in that area indicate that the ratio of grizzly bears to black bears is much higher. Groups of 11 grizzly bears have been reported there during this study, and scats counted on the roads in the more open stretches were predominantly from grizzly bears.

Discussion of Black Bear Ecology

The term "home range" can be defined in a number of ways, but generally, as in this study, it refers to an area in which an individual spends the greatest portion of its time (Burt, 1943). Most mammals make occasional sallies outside this area, but this type of movement is usually excluded when one is calculating home ranges. An investigation of home ranges was included in this study because knowledge of them is fundamental to an understanding of bear management and population regulation.

Most other estimates of black bear home ranges have been rather vague. Trippensee (1948) thought that the area a bear moved over was so large that it was not a range but a circuit, and Scott (1947) also said they travelled widely in search of food. Other estimates run from 10 to 20 miles in extent (Seton, 1929; Cahalane, 1947; Spencer, 1955). In recent studies in Wisconsin, Knudsen (1961) found that either sex would stay in a small area for a short time, but that the animals, especially the males, moved around considerably over a period of time. Erickson and Petrides (1964) said that Michigan bears had a minimum summer range of six square miles, but an annual range of 15 square miles, with female ranges 1/3 smaller and male ranges 1/3 larger than those averages.

Hayne (1950) points out that home ranges cannot be calculated for animals caught in traps that are in a straight line, and trapping only along roads on the study area did put some of the traps on Big Creek in straight lines. Trapping on a grid pattern, however, was simply impractical for so large an animal, and fortunately the roads did coincide with the bear habitat. Hayne also notes a relationship between the apparent home range and the distance between traps. I believe that both of these problems were adequately compensated for on Big

Creek with the observations of tagged animals, a method to which the bear lends itself and one which is superior to recapture data according to Davis (1953). Observations were relatively equal over the entire area.

The boundary strip method of measuring ranges (Stickel, 1954) and the observation-area curve method (Odum and Kuenzler, 1955) were not suitable for this study because both the bear habitat and the bear home ranges were strongly linear as a result of the linearity of the topography, and because true home area sizes were masked by the great elevational extremes within the home range of individuals. Stumpf and Mohr (1962) also have shown that many mammals and birds and even some reptiles normally have home ranges showing strong linearity. For these reasons, even though the analysis of home ranges based on distances between captures or observations also has biological and statistical deficiencies, I believe it the most suitable method for this study. The consistency of the home range sizes lends confidence to the method. The average maximum movements (Table 1) of 1.6 miles for females (146 locations on 31 adults) and 3.9 miles for males (83 locations on 16 adults) were below estimates from deciduous forest areas. Further refinements of the estimates would be meaningless, but the diameters of the ranges of both males and females, even if arbitrarily assumed circular, would give home ranges of 2.0 square miles for females and 11.9 square miles for males. These figures are still below the more conservative estimates based on the average of all movements for 29 bears by Erickson and Petrides (1964) and which also assumed circular ranges. Because many of the sub-adults were transients, their movements were not calculated. Sub-adult residents on the area were either with their mothers or grew into adults and were included in the study in that manner.

The great diversity of topography, climate, and vegetation on the Big Creek study area makes the small ranges possible by providing varied ecological conditions within small boundaries. There was a difference in the quality of habitat, but only because the one type was too high in elevation and had a climate too severe to be permanent bear habitat. Knudsen (1961) said that in Wisconsin the best black bear habitat is an area of diverse highlands and swamps. Trippensee (1948) stated, from general impressions, that rough terrain makes the best bear habitat because it provides dens, cover, and water. Small as home ranges are on Big Creek, they include areas that are important in early spring survival, but that are desert-like and devoid of food by late June. Other areas that are under deep snow until early summer are important to the survival of bears in autumn. There is an abundance of food in the stream bottoms and snowslides in early summer, and in late summer and fall the north slopes have many berries. High areas often have abundant food late in autumn.

Harlow (1961:491) suggests that bears in eastern North America move into areas when acorns are abundant. Drahos (1951) cites references of bears during colonial times making mass fall migrations into New York when food was scarce. Schorger (1949) lists numerous references in the early 1800's of bear immigration into areas of abundant food in Wisconsin, of mass spring migrations of bears to open grassland areas in southern Wisconsin and elsewhere, and of immense droves of bears accompanying buffalo movements in the fall. He concludes, however, that these probably were merely local movements and that years of high population density may have resulted in emigration because of intraspecific strife and insufficient food, and that this increase in emigration would explain the influx of bears into certain areas in some falls.

Except for the dispersal of sub-adults, nothing in this study indicated that bears under natural conditions make anything other than local annual movements. Sub-adults did move from the area, however, and in certain years this emigration may be higher. The long and predictable spring movements by two adult bears that had become accustomed to feeding in the Apgar and Big Creek Ranger Station garbage dumps illustrate that home range bonds can be circumvented under special conditions. Together with the reports of similar movements to spawning streams in Alaska by black bears and brown bears (Troyer, 1964; A. M. Pearson, 1965, personal communication), these data suggest that there may have been some truth in early reports of seasonal bear migrations. Erickson and Petrides (1964), however, found little difference between movements of dump and wild bears in Michigam. Nevertheless, bears that regularly made long movements before the advent of the white man in North America would no doubt have had a selective advantage in some areas, and the talent would have been easily transmitted from mother to cubs, either genetically or culturally.

The increased use by bears of road areas that were seeded and the use of such areas as snowslides, certain seral stands following burns, and dry meadows demonstrated that bears will move to food within their home range areas. The experiment with seeded strips clearly showed that bears can be made more accessible to hunters in this manner.

Erickson and Petrides (1964) could find little evidence of dispersal in bear populations in Michigan, although two yearlings moved about six miles each and an adult female and her cub moved 19.4 miles. Stickley (1961) reported a 2-1/2 year old male that moved 90 miles. The results of this study and the 90 mile movement reported by Stickley illustrate that there is dispersal of young black bears from the area in which they were born. With populations such as locusts, Kennedy (1956) says that entire populations move--the adults find the growth resources, and the juveniles exploit them. Many mammals travel in herds or packs in a similar manner, only in a large range. Animals such as bears, however, seem characterized by stable populations of adults tenaciously holding the most suitable habitat, leaving the young to try to fit into that habitat, or to search elsewhere for a suitable range.

Relationships between the species in an area must also be considered in a study of their biology and management, even if the species are seemingly indifferent to each other. If nothing else, they are at least mutual components of each other's environment. Modifications of the environment by one species might indirectly affect the other species; for example, black bears on a moose winter range about nine miles southeast of the Big Creek study area girdle lodgepole pines. The bears are merely after the cambium layer on the pines, but they have killed great numbers of the trees on the winter range. Their activity has tended to keep the winter range in a seral stage of lodgepole pine and willow, rather than to let it proceed to a *Thuja plicata*/*Pachistima myrsinites* climax, as described by Daubenmire (1953). The relationship between closely related species such as grizzly bears and black bears is even more crucial since they compete for some of the same food and because the grizzly bear is known to prey on black bears.

My studies suggest that in dense forests the black bear and the grizzly bear are compatible, and that in such habitat the black bear can reach far greater numbers than the grizzly bear. Why the grizzly, which is the dominant animal, can be numerous in the open country 30 miles farther north but scarce in Big Creek remains obscure. The black bear is perhaps less abundant in open country because predation by grizzly bears increases as the density of the forest decreases, but the destruction of grizzlies by man, which is thought to be the main control on grizzly numbers, is much easier in the northern, more open area where grizzly numbers are highest. The food habits of the two species differ somewhat in that grizzly bears prey more on other animals than do black bears. If black bears are important to grizzlies as prey, then grizzlies should be more abundant in Big Creek. Big Creek is less remote from human habitation, however, and perhaps the contact with man limits the grizzly there, while the black bear, because of previous heavy predation by grizzlies, avoids the more open areas to the north.

Denning during the winter appears to be universal in black bears in temperate and northern areas. I included a study of den ecology because I believed that variations in winter mortality rates might be important in population regulation of black bears. Gerstell (1939) said that in Pennsylvania bears den for four months and that farther south they den for shorter periods. Dalquest (in Rausch, 1961) stated that in Washington bears den for 5-1/2 months at high altitudes and for 2-1/2 to three months at low altitudes. Schoonmaker (1938) found that in New York bears den in late November or the first week in December, and Erickson (1964) found that in Michigan some bears start to den by early October, but that most bears den from mid-November to mid-April, a period of approximately five months. Aldous (1937) and Morse (1937) reported that bears leave their dens by mid-April in Minnesota, and Spencer (1955) said that in Maine they leave their dens the first two weeks in April.

Bears denned for longer periods in the Big Creek study than elsewhere. They usually denned earlier (approximately October 20) and came out later (early May). The causes that are involved in the timing and triggering of denning are somewhat obscure. Other authors believe the physical condition of the individual animal is most importamt. Rausch (1961) thought it possible that bears in poor condition do not den, and this may be true in coastal or southern areas. Matson (1954) says they den because they are "fed up" and may cease eating weeks before denning. He believes physical condition is more important than climate. Erickson and Youatt (1961) found that of four penned bears, a female that was in the poorest condition stayed active longest, indicating that physical condition was important. They agreed with the theory of Grinnell _et al_. (1937) "that the length of the period of dormancy is regulated by the abundance or scarcity of food." Johnson (1930) showed, however, that in ground squirrels starvation hastens hibernation, and Kayser (1965) concluded in his excellent review of hibernation that while internal conditions are eminently important, climatic and nutritive factors also are important in the induction of dormancy. Big Creek bears fed until forced to den by storms. Climatic factors apparently supercede endocrine, nutritive, or photoperiodic stimuli on Big Creek, even though such stimuli may condition the bears and should still be considered as possible triggering mechanisms in other regions that black bears inhabit.

Krott and Krott (1962) maintain that European brown bears have an innate daily and yearly rhythm and that they are true hibernators. They have little data to verify this statement, however. Black bears have in the past been commonly referred to as hibernators. The problem is largely a matter of semantics, and under a very liberal definition they will probably continue to be called hibernators. Hock (1960) and Erickson and Youatt (1961) have shown, however, that black bears do not have a great reduction in body temperature during winter like the true "deep hibernators." Hock reports a temperature drop of 7°F and Erickson and Youatt found a drop of 3 - 4°F; these temperatures are approximately 68°F higher than temperatures of the true hibernators during their deep dormancy. The oxygen consumption and energy expenditure of bears is comparable to that of true hibernators, however (Kayser, 1965). Some denned bears I observed shivered almost constantly even when unaware of being observed, something which the deep hibernators do only during arousal.

In a summary of black bear ecology, most bears on Big Creek have a strong attachment to home range areas which are smaller than heretofore reported, and this attachment has endured through at least seven years for four bears and eight years for another bear (No. 12). As shown on page 97, a form of territoriality seems to enhance this attachment. The adequacy of small home ranges on Big Creek seems dependent on the rough topography which creates a diverse climate and which in turn provides a diverse food supply in small areas. Apparently this need as well as the other habitat requirements of individual bears are met in other areas by larger home ranges.

CHAPTER FIVE

REPRODUCTIVE STUDIES

Bears are unique in North America in having the lowest reproductive rate of any land mammal, except possibly the muskox, and the reproductive rate of bears now appears even lower than previously suspected. The biological adequacy of this low rate stems partly from the competence of mothers and partly from the precocious nature of the young; even by the age of six months they are capable foragers and fighters. Erickson (1959) has shown that young bears in Michigan can survive if they are separated from their mothers at seven months of age.

Breeding Season

Females were found in estrus as early as May 25 and as late as August 10, with a peak in June (Table 3). Females with yearlings usually kept them close by until the peak of the breeding season. For example, two females with yearlings were seen on June 20, but when seen again in early July, each of them was then in the company of an adult male and without her young. One female was observed to be in partial estrus on June 23, however, while her yearlings were still with her. Nine adult females were examined during the peak of the breeding season and were found not in estrus, but three of these

Character	May	June	July	August
Vulval Swelling	2	25	12	6
Male-female Pairs	0	10	3	0

Table 3. The breeding season of bears based on the incidence of vulval swelling and male-female pairs.

had cubs with them. Five females that I examined were killed in Washington between June 12 and June 27 and all had mature follicles 8 to 12 mm in diameter. Corpora lutea were observed in another female killed in Washington on June 14, 1965. The earliest date that Erickson and Nellor (1964) observed corpora lutea in Michigan bears was July 20.

Thirteen male-female pairs were observed between June 1 and July 10. Female No. 19 was seen with males No. 62 and 116 on consecutive days, but no females were ever observed with more than one male in attendance.

Erickson and Nellor (1964) have shown that testicular activity in males does not start to decline until mid-September and that the activity has ceased by October.

Sex Ratios

On the Big Creek study area the sex ratio was 112 males: 100 females captured between 1959 and 1966 (Table 4). While the sex ratios of the adults and cubs were even, the number of 1-1/2 and 2-1/2 year old and sub-adult males captured on the area was almost double the number of similarly aged females. The ratio was 192:100, or 35 per cent females. This difference is significant at the one per cent level by the Chi-square test.

Minimum Breeding Age

No bears younger than 4-1/2 were observed in estrus. Table 5 shows that on Big Creek two females were at least 5-1/2 years of age, two were at least 6-1/2 years of age,

Age	Sex M	F	Total	Percentage that were Females
Cubs	8	10	18	55.6*
1-1/2 & 2-1/2 yr. olds	19	12	31	38.6
Sub-adults	29	13	42	31.0
Adults	26	38	64	59.4*
Total	82	73	155	47.1*

*These do not deviate significantly from an even sex ratio by the Chi-square test.

Table 4. The sex composition of bears captured on the Big Creek study area during the period 1959 to 1966.

Bear No.	Minimum Age* At First Estrus	At which Bear was last observed without Cubs	At which Bear had her First Cubs
4	4-1/2	6-1/2	Unknown
10	Unknown	7-1/2	8-1/2
61	Unknown	5-1/2	Unknown
71	Unknown	5-1/2	6-1/2
113	4-1/2	6-1/2	7-1/2

*Several of these animals may have been one or more years older than indicated in this table.

Table 5. The minimum breeding age of female bears on the Big Creek study area.

and one was at least 7-1/2 years of age without having ever raised a litter of cubs. The possibility that some young bears may breed successfully but lose their young in early spring was indicated by female No. 4. She was first captured when she was a minimum of 4-1/2 years old; when she was recaptured the next year in July, the condition of her mammae showed some development, but she did not have young with her then and she was in estrus.

Litter Sizes

A summary of the litter sizes reported for this and other studies is presented in Table 6. The average litter sizes for the Big Creek study were based on both capture and observation data, but the rest of the Montana observations were recorded by personnel of the Montana Fish and Game Department, the United States Forest Service, and Glacier National Park. Their observations were restricted to the last week of July and the entire month of August, a period when very few females still have yearlings with them. Yearling litter sizes were based on Big Creek data. The data for the other studies cited were collected in various ways such as capture, observation, hunter kills, road kills, and newspaper accounts. On Big Creek, 29 black females had 1.6 cubs or yearlings per litter, and 16 brown females had 1.7 cubs or yearlings per litter.

Corpus luteum and mature follicle counts were also made from black bear reproductive tracts collected on the

Area	Total Bears	Cubs/ 100 Adults	Family Groups	No. of Young	Av. Litter Size
Montana					
Cubs			38	66	1.7
Big Creek					
State-Wide Survey					
1961	189	12	33	59	1.8
1962	471	20	53	80	1.5
1963	123	34	18	29	1.6
1964	248	26	28	48	1.7
1965	311	21	34	54	1.6
	1,342		203	334	1.6
Yearlings			23	36	1.6
Maine (Spencer, 1955)			38	-	2.4
Florida (Harlow, 1961)			10	-	2.2
Michigan (Erickson and Nellor, 1964)			20	-	2.2
Alaska (Erickson and Nellor, 1964)			23	-	2.0
Wisconsin (Schorger, 1949)			284	-	2.4
Virginia (Stickley, 1961)			19*	-	2.6
Captive (at birth) Baker (1912)			-	-	2.4

*Embryos and cubs are included in this total.

Table 6. The number of cubs per 100 adults in Montana, and the average litter sizes for the Big Creek study area, for all of Montana, and for other study areas.

Big Creek study area and in western Washington. They are compared in Table 7 with similar data collected in Michigan by Erickson and Nellor (1964) and in Virginia by Stickley (1961). The numbers of mature follicles were also counted because, as Erickson and Nellor (1964) pointed out, the black bear is an induced ovulator, and near the peak of the breeding season several follicles attain mature size. At that time they can be counted as easily as the corpora lutea after ovulation. Two bears had both corpora lutea and atretic mature follicles, however, indicating that the number of unruptured mature follicles is likely to be in excess of the number of follicles actually involved in the ovulation rate.

Frequency of Litters

Two bears on Big Creek had two litters each within a three year period. Nine other adult females had no litters for at least two consecutive years, and two females skipped three years. As shown in Table 8, the percentage of females accompanied by cubs was also low every year except 1959 and 1964. None of the 39 marked adult females observed or captured on Big Creek during 1961, 1962, and 1963 had cubs with them. Some unmarked females observed on the area during those years had cubs, but the ratio for the entire population must have been very low.

Area	No. of Female Tracts	Av. No. of Mature Follicles	Av. No. of Corpora Lutea
Washington and Montana			
Early June	8	2.0	-
June to December	16	-	1.9
Total	24	-	1.9*
Montana only	5	-	1.8
Michigan	12	-	2.4
Virginia	22	-	2.4

*Mature follicles and corpora lutea.

Table 7. Corpora lutea counts from Montana, Washington, Michigan, and Virginia. Mature follicle counts from Washington.

Year	Females: Total No. Captured or Observed	No. with Cubs	Percentage with Cubs
1959	13	5	38.5
1960	16	3	18.8
1961	18	0	0
1962	9	0	0
1963	12	0	0
1964	10	4	40.0
1965	14	2	14.3
1966	4	1	25.0
Total	96	15	15.6

Table 8. The numbers and percentage of marked adult females with or without cubs on Big Creek 1959-1966. Reproduction or survival of the young was very low from 1961 through 1963.

Discussion of Black Bear Reproduction

The reproductive capacity of Big Creek bears seems to be far below the potential for the species. Lack et al. (1957) believe that in birds the clutch size is limited genetically, on the average, to correspond to the brood size which produces the greatest number of surviving young, but that the size does change in response to changes in the habitat. In mammals, too, small families survive more successfully, and the litter size is controlled genetically. Cheatum and Severinghaus (1950), Jenkins (1963), and others have shown that the reproductive capacity of a species can vary with differences in nutrition and that these variations are expressed in changes in the ovulation rates, frequency of litters, minimum breeding age, or the early mortality rates of young. Lord (1960:496) has suggested that among mammals the "hibernators" have even smaller litters than non-hibernators because the survival rate of hibernators is higher. Apparently similar forces explain the adequacy of the low reproductive rates and poor survival of young in Big Creek black bears.

The length of the mating season in seasonal breeders such as bears normally has little significance in determining reproductive rates since under no conditions can second litters be propagated, nor can remating occur if pregnancy fails. The species is genetically isolated from such capabilities, and is adapted to the most favourable time of the year for breeding and bearing young. There is no indication that bears come into estrus more than once a year, but the time of estrus does vary considerably and might be significant in reproductive success because of local ecological conditions. There is even some evidence that the types of food eaten may be involved (see Appendix 3).

It has been generally believed that black bears mate in late June or early July (Baker, 1904; Rausch, 1961; Grinnel _et al_., 1937; Erickson and Nellor, 1964). Stickley (1961) and Knudsen (1961) state that the breeding season extends from June to early August. The breeding season in the Big Creek area seems to last longer than that reported elsewhere, although the June - July peak coincides with the season reported in other areas. Perhaps not enough data have been collected in other studies to determine the full length of the season, but, alternatively, the wide range of climatic conditions on Big Creek may extend the estrous cycle.

The apparent long breeding season on Big Creek could be deleterious to some bears, since females coming into estrus too late in the year might be in estrus at a time when most adult males have moved higher into the mountains, a condition analogous to the condition in fur seals (_Callorhinus ursinus_), where the females must come into estrus when they are on the islands with the males (A. M. Craig, 1966, personal communication). Prell (1930) has reported the occurrence of pseudoestrus in polar bears and brown bears following the regular estrous cycle, and this may be an alternate explanation for the apparent long breeding season in black bears, but other authors don't agree that polar bears have a pseudoestrus period.

Knudsen (1961) in Wisconsin and Erickson and Petrides (1964) in Michigan found the sex ratio in black bears to be even. Only when bears were trapped at dumps did the males outnumber the females, and this they attributed to a tendency of females to avoid other bears and man. The Michigan study also showed that 36 per cent of the cubs were females and that 55 per cent of the yearlings were females. Considered in relation to their sample sizes, however, the difference from an even sex ratio was not statistically significant. Stickley (1961) found an even sex ratio in Virginia, but Spencer (1955) found that of 236 bears killed in Maine, only 42 per cent were females. The unusual preponderance of males in the yearling, 2-1/2, and sub-adult group on Big Creek could result from higher mortality rates for female cubs during the first winter without their mother, but this explanation seems unlikely as the even sex ratios for adults would then have to be explained in some other way. Also, as the section on growth (p.108) shows, the weights for females and males were approximately equal during that period. The disparity more probably results from the movement of young males through the area at a greater rate than females of the same age; my records of dispersal do show that it was primarily young males that moved away from the area. The figures from Maine showing a ratio favourable to males were based on animals killed by hunters and probably merely indicate a selection by hunters for larger bears. Because males have larger ranges, there would also be a statistical tendency for hunters to kill a disproportionate number of males, just as Layne (1958) found the fox ratio in Illinois high to males when the females were on small home ranges near their dens during April and May. There probably is not a differential birth rate or natural mortality rate between the sexes of sub-adult black bears, therefore, and the low ratio of females is apparently only illusory as a result of the large number of transient sub-adult males crossing the area.

The minimum breeding age also is important in determining reproductive rates. Stickley (1961) reported a captive female black bear that apparently bred successfully at 2-1/2 years of age. Erickson and Nellor (1964) said that both sexes reach puberty at 3-1/2 years of age, and Baker (1912) listed three captive females that had their first cubs at 4-1/2 years of age. Rausch (1961) found that two captive females held in outdoor pens had their first cubs at 4-1/2 and 6-1/2 years of age. On the Big Creek study area, the minimum breeding age appeared to be higher than that for captive bears or Michigan bears. Wild black bears in the spruce-fir forest of Montana reach sexual maturity by the time they are 4-1/2 years of age, but they are not successful in raising litters before 6-1/2 to 7-1/2 years of age. Nutrition may be involved, since in mature domestic animals it does affect both sexual maturity (as measured by first ovulation) and the ovulation rates. The best known example of the latter is that of placing sheep on a high protein diet prior to breeding time to increase the ovulation rate. This slow sexual maturation or late breeding in bears no doubt lowers the reproductive rate of the population considerably. Failure to develop mature follicles is a likely cause, especially among young adults. The actual mechanisms involved are discussed below and in the sections on behaviour and on growth and development.

Litter sizes of black bears may be variable in different areas. Rowan (1945) found black bear litters of three to be common in Jasper National Park, Alberta, and says litters of four, five, and six have been observed. Most studies have reported average litter sizes in excess of two. My data on litter sizes and corpora lutea counts show conclusively that litters on Big Creek, throughout Montana, and in western Washington are smaller than in eastern North America. The small amount of data available on Alaska black bears also corresponds to those of Montana and Washington.

Brambell (1948:385) says that there are no adequate methods of determining litter sizes, but indices to litter size can still be useful. Estimates of litter size based on observations during this study should be more reliable than those for many of the other studies, since the state-wide survey was made at a time when cub and yearling family groups would not be confused. Data from other studies probably give minimal estimates because they include an unknown number of yearling family groups. On the other hand, those studies that were based on volunteered data no doubt contain a disproportionate number of larger litters, since people are more inclined to remember and report large litters.

The growth rate and adult weight of western bears may be involved in the smaller size of litters. MacArthur (1948) using laboratory house mice (Mus musculus) selected for large and small body size for 21 generations and produced a large and a small strain of mice that differed almost 100 per cent in average litter sizes. The smaller strain had the smaller litter size. Black bears on Big Creek apparently are restricted nutritionally as compared with bears elsewhere, which could account for their smaller average number of corpora lutea compared with eastern bears. This reduction in fecundity also may have a purely genetic cause, however, since it was constant throughout the West. The effect of the smaller litter sizes on overall reproductive rates seems significant, but it would not cause fluctuations since it is constant amnually. Whether this restriction on litter size corresponds with the largest number of young which can be raised successfully, as Lack (1956) proposes for birds, is open to further question.

The frequency of litters in Big Creek bears also is low compared to other areas. Drahos (1951) reports a female black bear in the National Zoological Park that had a litter every other year and only stopped breeding at 24 years of age. Stickley (1961) reports that 48 per cent of 38 wild adult females in Virginia had litters annually. The frequency of litters on the Big Creek study area was only 16 per cent annually.

Rausch (1961) and Wimsatt (1963) have shown that estrus can be induced every year if the cubs of the year are taken from the mother prior to the breeding season. Since black bears normally keep their young with them until they are 1-1/2 years of age and since lactation apparently inhibits breeding when the young are 1/2 year old, 50 per cent of all adult females from any population should have cubs with them. In Virginia, Stickley found such a percentage, and on Big Creek during 1959 and 1964 the percentage did not vary statistically from such a ratio. During 1961, 1962, and 1963 reproduction approached zero on the Big Creek area, however, then increased again in 1964 and 1965. This failure to produce young at proper intervals during 1961-1963 is discussed further in the sections on behaviour and population regulation.

CHAPTER SIX

DEATH RATES AND CAUSES OF MORTALITY

Forty-two bears from the Big Creek study area were killed by man between June, 1959, and May, 1966, one yearling in a trap was killed by an adult bear, and seven were killed accidentally or for study. The total number known to be dead is fifty.

Causes of natural mortality within the Big Creek population are still obscure. The remains of dead bears are not found scattered obviously on open winter ranges as are those of the large herbivorous mammals, nor are they found in scats or castings, as for small mammals. They must generally be consumed completely by other animals, or else they die in areas where their remains are not easily seen.

Mortality Rates

Early in the study I noted from preliminary data that either the fecundity of Big Creek bears was far below the potential reported from studies of zoo animals and of wild bears in eastern North America or else prenatal and early mortality rates were unduly high. In searching for early natural mortality, I found little conclusive evidence. Bears may be prone to prenatal mortality, however, because they have a long delay before implantation, and during this delay the blastocysts are vulnerable to a variety of mortality factors. Detection of these losses in a natural bear population is difficult. Throughout the study 68 per cent of the females potentially pregnant did not have young through failure to ovulate, prenatal mortality, or early mortality (Figure 13). The loss from the potential through failure to breed is indistinguishable from mortality before birth and thus is also accounted for in the survival curve.

Cubs fared well during their first year, with only 13 per cent dying between 1/2 and 1-1/2 years of age (see page 107). This percentage includes one cub whose mother was killed on July 20 and one cub that probably died as a result of injuries suffered during capture. If these two are excluded, then only five per cent of the cubs died between 1/2 and 1-1/2 years of age (Figure 13). This low mortality rate for cubs probably begins soon after birth, but information is difficult to obtain before the young are 5 - 6 months of age. Whole family loss was not observed, but such loss could increase mortality rates for cubs without detection.

As shown in the section on age structure (page 121), young bears over 1-1/2 years rapidly disappear from the population. Because an undetermined number of the older sub-adults dispersed from the area, true mortality rates could be calculated only for the more sedentary cubs and adults, while the sub-adult rates in Figure 13 include both death and dispersal.

The annual mortality rate of 14 per cent for adults is based on animals marked initially as adults and on sub-adults

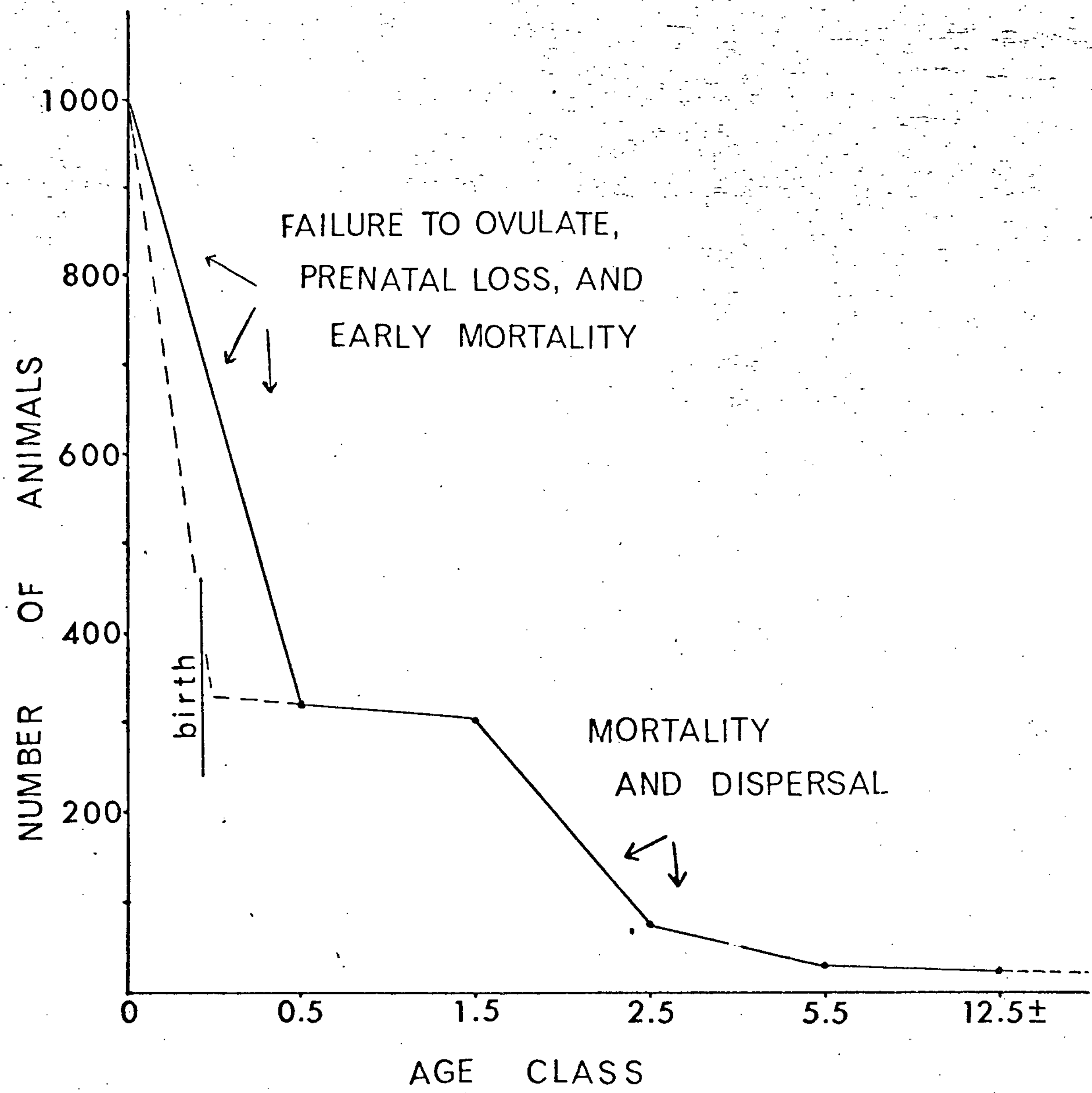

Figure 13. Survival curve for bears on the Big Creek study area based on estimated and measured mortality rates. Loss prior to birth is based on a potential 50 per cent pregnancy rate for adult females. An unknown amount of dispersal is included in the figures for 1-1/2 to 5-1/2 year old animals. The broken line running to birth and to 0.5 years represents the probable true curve for that period.

that grew to be adults during the study. Death rates were calculated and then totalled for 157 animals 5-1/2 years or older during 1960 through 1965. Bears killed by hunters or as a result of this study were excluded from this calculation.

Causes of Mortality

Denning Period. Through 1966 I have periodically checked the condition of 31 denned bears during the winter, making a final check of the den in May. Two cubs, eight yearlings, and 21 adults were observed. No mortality was recorded, nor did any of the bears appear to have any difficulty.

Parasites and Diseases. Ectoparasites are apparently the primary form of parasitism on the Big Creek bear population and so were included in the mortality studies. I examined 117 bears on the study area, and during May and June every bear examined had infestations of ticks (*Dermacentor andersoni*) on the neck and shoulders. Some adults had only a few, but many of the sub-adult bears often had 2 - 6 per square inch on the neck and shoulders. Thirty-six bears on the Big Creek study area and all bears from surrounding areas examined later in the summer or fall were free of ectoparasites. Two bears on the study area had fleas (*Arctopsylla ursi*, Rothchild, 1902), and two bears collected outside of the study area had extremely heavy infestations of ticks, fleas, and lice (*Trichodectes pinguis euarctidos*, Hopkins, 1954), with the lice in the thousands. These data suggest individual variation in susceptibility to ectoparasites, but there is also a geographic variation in the distribution of the parasites. King et al. (1960) examined 306 black bears in New York and found only two ticks of the genus *Ixodes*; Rausch (1961) found no ectoparasites on Alaskan black bears. The bears on Big Creek apparently acquire great numbers of ticks while feeding on south slopes or dry meadow areas in the early spring. Since the sub-adults are in poorer condition than the adults at this time of year, they probably have more difficulty in getting rid of ecto-parasites. Kartman (1942) has shown that rats receiving rations high in Vitamin A and B_2 rid themselves of lice, while control animals do not.

Adults of the nematode *Dirofilaria ursi*, Yamaguti, 1941, were found in two of the bears killed on Big Creek. This parasite is common in New York; King et al. (1960) found microfilariae in 104 of 109 bears examined. Rausch (1961) found adults of this species in only one black bear in Alaska, but it is common there in the brown bear. The tapeworm *Taenia saginata* was collected occasionally from black bear scats on Big Creek. The infections probably arose when the bears ate meat scraps at the Ranger Station and in the trapsites. Numerous hookworms (probably *Uncinaria yukonensis*) were found in the small intestine of an adult female killed in December, 1964.

Diseases are uncommon in black bears. No diseased animals were found in the Big Creek population, and Rausch (1961) in Alaska and King et al. (1960) in New York found black bears in those areas largely free of diseases. Parasites and diseases no doubt contribute to some deaths, especially among sub-adults, but they were not found important in this study.

Predation. Grizzly and black bears are often seen in groups when feeding in garbage dumps, but three cases of grizzly predation on black bears during the summer and fall were noted in the vicinity of the Big Creek study area. A yearling in a trap was killed and eaten either by a large male black bear or a grizzly. The adult chased from the carcass appeared to be a large black bear, but positive identification was not made. One black bear scat collected on the Big Creek area contained the remains of a cub, but this might have been merely carrion eating (Tisch, 1961). Carcasses of black bears accidentally killed during the study were routinely used for bait and were readily consumed by other black bears at all seasons of the year. I was also informed of two cases of black bear predation on smaller black bears in Yellowstone Park (M. G. Hornocker; 1965, personal communication).

Hunting Pressure. Of 37 bears marked on the Big Creek study area in 1959, only one was shot that same year. In 1960 publicity given to the area and public education on the methods of hunting bears increased the hunter kill to 13 per cent of 47 bears marked that year. Hunting success increased rapidly and over the next few years 24 per cent of the bears marked in 1959, 42 per cent of the bears marked in 1960, and 24 per cent of those marked in 1961 were eventually taken by hunters. From 1964 through 1966 the season on bears was closed in the Big

Creek study area, and only two of 32 bears marked during 1964 and 1965 were shot in surrounding areas.

Other mortality. Seasonal variation in behaviour makes bears vulnerable to hunters, especially in the spring and early summer when they are feeding on the dry meadow areas (page 87). Individual variation in behaviour contributed to the death of one bear when it constantly visited a trapsite and was finally spotted and shot by a hunter.

The climate of the Big Creek area is probably indirectly involved in mortality. The longer denning period found in this study shortens the length of time each year during which bears can feed (see section on growth and development). Poor nutrition could, therefore, cause the smaller size of Big Creek bears compared with bears of other areas, and in this way mortality rates, especially for sub-adults, may be influenced by climate.

Discussion of Mortality in Bears

Brambell (1948:387) indicates that loss of eggs through non-fertilization is rare in most induced ovulators. No embryo-corpora lutea ratios have been calculated to determine whether ova were ovulated but not fertilized, but some non-fertilization must result from failure of mature follicles to ovulate (see section on reproduction, page 66 and Appendix 3 for possible causes).

Uterine mortality has been reported by Hansson (1947) as being "high during late pregnancy" in the mink (Mustela *vison*), at approximately 32 per cent in the gray fox (*Urcyon cinereoargenteus*) by Layne (1958), and as high as 43 per cent during the first half of pregnancy in the wild rabbit (Brambell, 1948). Nalbandov (1964) says 30 to 50 per cent of the fertilized eggs are lost during gestation in domestic and laboratory animals. Losses probably vary between species, especially among polytocous animals, and losses are generally higher in species with high ovulation rates (Hammond, 1921). Bears not only have small litters normally, reducing the possibility of uterine loss, but the pregnancy period coincides with the period of abundant nutrition for the bear. The opportunistic food habits of the species seemingly would ensure an adequate food supply of some sort during summer and autumn in almost any type of bear range. The rapid gain in weight from mid-July until fall by all bears on Big Creek supports this view. Krott and Krott (1962) state that hunger is the only natural check on European brown bear populations, but they have little information to substantiate this statement. Even in poor berry years Big Creek bears made significant gains in weight during autumn. The correlation of high and low reproductive rates of Big Creek bears with good and poor berry years is contrary evidence, however (see page 113).

Nothing is known about parturition losses of the black bear, but since the mother bears are as competent as other mammals and the new-born are small, these losses are probably low. Postparturition loss of the young before the bears leave their dens is also difficult to evaluate. The similarity of average corpora lutea counts and average litter sizes indicates that if many young are lost, the loss must generally involve whole litters. Brambell (1948:396) said that the loss of single embryos out of a litter is usually intrinsic (genetic), while loss of whole litters is probably caused by extrinsic events affecting the maternal environment.

Mortality rates for bears 1/2 to 1-1/2 years of age are low, but once the young are separated from their mothers at 1-1/2 years, losses increase rapidly. Hornocker (1962) also showed that survival in grizzlies was high as long as the young were with their mothers. Occasionally black bears retain their cubs for longer than 1-1/2 years as do polar bears (Harington, 1964) and grizzly bears, and this may prolong the period of low death rate. Sub-adults separated from their mothers apparently succumb at a faster rate to all of the decimating factors mentioned in this section.

Adult bears are stable in the population, and no natural mortality was observed. At some point in the life of adults mortality might increase significantly, but further data are required to determine if this occurs or if death rates stay constant for all adults. In general, adults seem well adapted to the Big Creek habitat.

Kurtén (1958) reports a high winter mortality in cave bears, as shown by the skeletal remains in caves, and Wright (1910:67) claims to have found the carcasses of many black bears in their winter dens. Despite these claims, mortality during the denning period must be low. Bears survive well even in the spruce-fir forest where climatic changes force them to den before they become satiated.

Schorger (1949) said that in the past timber wolves were the chief natural enemy of black bears, especially in the winter. Boyer (1948) reported that two coyotes in California attacked and killed a sub-adult black bear that was denned under a fir, and in this study two coyotes were seen chasing an adult male black bear, although the chase seemed casual, too playful for predation. Some smaller bears on Big Creek were killed by larger black bears and grizzly bears. According to Rausch (1961), there is a widespread belief in Alaska that grizzly bears prey on black bears, and evolutionists hold that the black bear evolved as a forest animal to avoid grizzly predation. Erickson (1957) reported that a cub in a trap was killed and eaten by an adult black bear, but he believed that since bears in his study did not eat the remains of other bears in the fall, they preyed on smaller bears only during the spring and only because of extreme hunger. On Big Creek, bears ate the remains of other bears when the opportunity arose.

Apparently man has always been a predator of bears and of course he still is today. Stickley (1961) found that 33 per cent of the bears he trapped and marked in Virginia were shot by hunters the same fall. My study has shown that this form of "predation" can be easily increased or decreased in the management of bears.

The overriding evidence of this study is that the low pregnancy rate of adults and the high mortality rates of sub-adults account for most of the loss in total population numbers. Food quantity and food quality seem responsible for annual changes in the rates and the climate of the area dictates ultimately what these levels are, but behaviour, parasites, and predators also alter or contribute to changes in the rates.

CHAPTER SEVEN

BEHAVIOUR

Several aspects of bear behaviour observed during this study are important in the survival of bears and in the regulation of bear numbers. They are agonistic behaviour, family relationships, seasonal and daily changes in behaviour, territorial behaviour, and individual variation in behaviour.

Agonistic Behaviour

The observations made on free-ranging and trapped wild black bears during this study indicate there are at least two and probably three forms of agonistic action directed toward man and toward other bears. The first type, a sudden protective lunge and swat, comes with little warning that humans recognize. Some bears are silent prior to this movement, but all give a loud warning "huff" concurrently. Other individuals give an extended, variously pitched, and rather subdued growl prior to this action; they may prolong this vocalization with a low growl, "chopping" of the jaws, and some huffing following the lunge. They will sometimes alternate these actions with attempts to flee. Drahos (1951) considered black bears as most demonstrative in their facial, body, and vocal expressions, but Lorenz (1953) stated that because bears are solitary animals, their social relations are poorly developed, the thick skin of their face is sparsely furnished with muscles of expression, and they strike suddenly without warning, rather than laying back their ears and snapping with their jaws like other large carnivores. Lorenz evidently observed the first type of agonistic behaviour that I described.

The second form of agonistic behaviour is a sudden swatting and biting attack, with the bear rushing straight toward the opponent. The charge often terminates with the body raised and the bear striking with one or both front paws. This motion is usually preceded by huffing, chopping of the jaws, extension of the upper lip, and sometimes by laying back of the ears. Initially, the anterior part of the body is moved slowly towards the opponent to maneuver into an attacking position. They do not snarl or curl the lips. More warning is given before this second type of attack, but under both forms the huffing is as meaningful as the familiar growl or snarl in the canids. The discrepancies between my observations and previous reports probably arise from differences in individual behaviour among bears and from differences between wild and zoo bears. Failure to give warning before this attack seems to arise from two situations or causes: (1) the bear practicing deceit (this is rare); (2) the opponent unexpectedly approaching closer than tolerated.

The third type of encounter resembles a ritual. It has been described in grizzlies by Hornocker (1962), in Yezo brown bears (U. a. yesoensis) by Masatomi (1964), and it also has been observed in wild black bears. The threatening animal assumes a sideways stance which the opponent recognizes. Most of these encounters end with the second bear fleeing or moving away before an actual attack is made.

Family Relationships

On two occasions during this study females held in a trap were observed to allow their young to suckle. Erickson (1957) reported a similar observation in Michigan bears. That female bears are harsh in the application of discipline to their young is common knowledge, but they can also be quite indulgent when the family feeds together and when the female is nursing or training the young. During the winter when the cubs are one year old the female and the young crowd together in the den. When they are disturbed, there is a constant movement by the bears to seek the warmest and most protected position.

Females do not always protect their young against man; Knudsen (1961) and Erickson (1957) also found this to be true with Wisconsin and Michigan black bears. However, a free-ranging female repeatedly attacked my assistant and me while we were capturing and tagging her young. She had to be subdued before we could continue the work. This defense of the young is, under some conditions, directed against adult males. A trapped yearling was killed and eaten, apparently by a large black male. The mother of the yearling and another yearling were either in or near trees about 60 yards away from the trap-site when the large bear was chased from the carcass. The crushed vegetation indicated that the female had spent most of the night and morning attempting to rescue the yearling. Wide trails indicated she had approached repeatedly, only to be chased back to the safety of a large spruce. The transformation of the area from a lush meadow with vegetation about two feet high to a completely trampled area showed a vast amount of activity in approximately 12 hours.

The females are tolerant of the young until they are at least 1-1/2 years of age. Erickson and Nellor (1964) reported that cubs normally are weaned in September, but one instance of a female feeding a 16 month old yearling in May was observed during my study. This observation was made in the upper part of the drainage at about 6,500 feet in elevation. None of the females captured when accompanied by yearlings appeared to be suckling young.

Usually just at the onset of the breeding season in late June, the young are no longer seen in the company of the female, but in one positive case and two probable cases yearlings were observed in close company with the mother after the breeding season. In all three instances the family groups were residing at the extreme upper limits of permanent female ranges at 6,000 to 6,500 feet. Six other family groups on the area broke up in late June to early July. Two groups were seen on June 23, but one of the females was seen again on July 7 without her yearlings. Murie (in Schorger, 1949) reported that three yearlings in Yellowstone Park rejoined their mother for a short time after the breeding season, but the situation may not be comparable. She did show maternal behaviour after the breeding season, however, which corresponds to my data.

Some females will tolerate or are indifferent to yearlings on the mother's home range even after the family group has separated. Dispersal of 1-1/2 year old young from the area has been noted, but seven litters of young were observed on their mothers' home ranges after the family group had broken up. Much of the overlap in bear home ranges may originate from these blood relationships.

Communication within the family group seems to be primarily huffing and swatting on the female's part, but small cubs squall considerably when hungry or uncomfortable and voice a "purr" when comfortable or seeking comfort. The purr resembles a rapid series of grunts, rather than the internal purr of cats. Meyer-Holzapfel (1957) has described this behaviour further. When older, the cubs frequently voice a pleading bawl to the mother, and on one occasion I heard this call used in communication between two yearlings. One female voiced a subdued "pump pump pump ..." call, repeated continually to a cub held in a trap. The call seemed directed to the cub and not at the handlers.

<u>Seasonal Changes in Behaviour</u>

Schoonmaker (1938) reports seeing six black bears in a group in the wild, but observations during this study indicate that under wild conditions in Montana individual bears or individual family groups seldom approach one another during most periods of the year. An adult female was observed to flee from an approaching adult male and stay about 100 yards from him while feeding, although it was only one month before the breeding season. Eleven bears observed over a 10 day period in the China Basin area of the Big Creek drainage kept at least 50 yards apart at all times. This distance appears to be mutually sought. Three cases of sub-adult males or adult females moving cautiously away from large males were observed. A confrontation between two bears was observed on a ridge where air currents probably prevented any advance warning, and after one rush by the dominant bear, both individuals withdrew to proper distances. During the breeding season, however, adult males and females pair and travel or feed side by side for several days at a time.

A seasonal change in behaviour occurs during the denning period also. Most bears observed during the winter have been extremely tolerant of the observer, allowing approaches to within two feet without exhibiting any agonistic behaviour. Three bears, however, attempted to bite the tagging pliers when attempts were made to place tags in their ears, and they had to be subdued with drugs before they could be marked. Other studies have shown a similar reduction in sensitivity (Aldous, 1937; Morse, 1937; Matson, 1954). During this study only two bears out of 40 observed during mid-winter showed considerable agonistic behaviour. Both were adult females, and at least one had young within a month, indicating that reproductive condition may be involved in mid-winter agonistic behaviour. Another definitely pregnant female killed December 21 made no attempt to attack, however. Two other bears made rushes to the den entrance when observed, but both of these observations were in mid-May. Since these bears were the only two bears observed in dens late in the spring and since they both rushed at me, I concluded that there is again a marked behavioural change before bears leave their dens.

Two bears did not exhibit any unusual behaviour when observed, but when the dens were checked three weeks later, both had left even though it was mid-winter. I tracked one of the animals for about three miles, but while her direction remained constant as if she were heading for a definite site, she did not enter another den. She did survive the winter, since she was in the original den the following year.

One denned bear being tagged ran from the den and climbed into the branches of some tall bushes. The bear was easily subdued with drugs, but it was quite competent in climbing and fighting before it was drugged. The temperature was near zero, and there were about nine feet of snow in the vicinity of the den.

Winter behaviour of bears seems directed at regulating their temperature. Whereas true hibernators are only awake 7.5 per cent of the time (Kayser, 1965), bears seem to be awake most of the time. During all but one of my 42 observations, the bears were aroused enough at least to raise their heads or bodies slightly and look out. This activity was generally accompanied by shivering or by slow movements to return to the curled position. This winter behaviour becomes dominant early in the fall. A female with eight month old cubs was observed under a large Douglas fir on October 7, and though not denned, they showed great reluctance to move out into the wet foliage. I approached and observed them several times from about 80 feet.

There are seasonal and daily changes in feeding behaviour also. Numerous references in the literature state that for some time after emerging in the spring bears do not eat (Aldous, 1937; Matson, 1954; and others), but no such behaviour was noted in this study. Bears were observed feeding on open areas as early as late April and early May. During early spring Big Creek bears did show a much greater tendency to lie down frequently while feeding, however, while during September bears were observed to feed continually for up to six hours on rather dull or cool days. All bears were more active during the early morning periods and after 6:00 p.m.

Territorial Behaviour

In addition to their home range attachments, bears appear to direct a type of territorial behaviour toward certain other bears. Even though some home ranges overlap completely, bears do not move laterally into other occupied areas. They do, however, move out of their own range into "vacant" areas at higher elevations. The high ratio of males in the 1-1/2 and 2-1/2 year old group also indicates specific territorial pressure on males of this age with subsequent increased movement of transient young males through the area.

Fixed routes and "bear trees," which are generally accepted by ethologists as important in the ritualization of agonistic behaviour (Etkin, 1963:8), were observed throughout the area. Such behaviour often took the form of defacing or destroying signs and markers erected by man.

Individual Variation

Behaviour varies greatly within the population. Some of this variation is probably genetic, but much of it appears to be learned.

Many animals are completely docile when first captured, and if they are not injured, they often become quite accustomed to the trap and to the handling procedure on subsequent captures. One yearling actually became habituated to one of the trapsites, willing to endure the discomfort of the steel trap for the small reward of the bait. It became necessary to remove the trap from that site until the bear ceased waiting by it. The docile types usually sat quietly without fighting the trap, and when approached, they tried to hide under logs or behind their paws. The drug could often be administered with a hand syringe to small bears of this type.

Some animals were highly excitable and contributed to their own agitation by injuring themselves attempting to escape. This type of animal was also far more prone to agonistic behaviour. In some cases this behaviour may have been precipitated by an initial injury in the trap, but numerous animals were of this type without apparent provocation other than being trapped.

The greatest variability was in learned behaviour. While most adult bears remained on small home ranges, two adults (one male and one female) made regular 10 mile movements between a dump at the Ranger Station by the mouth of Big Creek and Apgar Village in Glacier National Park. Since other bears resident within one mile of the Ranger Station on the study area did not frequent the dump, this behaviour was evidently learned. Krott and Krott (1962) said the European brown bear could not learn to recognize sources of danger, but in this study trapping success demonstrated a considerable measure of learning by wild bears. Other species, such as rats or coyotes, simply avoid unfamiliar objects in their home range areas, but with bears the trap became an object to be circumvented through new approaches to the bait. Many animals became so proficient at taking the bait without being captured that elaborate placement of additional traps was necessary to make recaptures. Some of the animals lost their talent over the winter and were easily captured in the following year, but others remained proficient at stealing bait from year to year. Tracks showed that some bears avoided the trapsites completely after several captures.

Discussion

The behaviour of many animals is intimately involved with their survival, reproduction, and population regulation. This study has shown that this is true of the black bear. Behavioural observations have been an aid in understanding certain other aspects of bear biology. For example, the ecological data have shown that home ranges can be small, but they have not shown why they are small. Social inhibition of movement and tolerance of close neighbors seem to be the primary reasons.

Agonistic behaviour in black bears is much more highly developed than previously recognized. Etkin (1963:4) stated that aggressive potential is usually the deciding factor in survival but that social life is common in higher vertebrates even so, since a social group offers many advantages to individuals. This general statement seems applicable to bears. Black bears do not form groups outside of the family group, but they do live permanently in small areas in association with other bears. Ritualization of agonistic behaviour and communication becomes necessary under such conditions. This study shows that black bears have many vocal and body expressions that are important in avoiding actual conflict, in establishing territorial rights, and in communicating within the family groups.

Family behaviour, or "care-dependency" behaviour, as it is referred to by Scott (1958), gives rise to a cultural inheritance. This behaviour is well-developed in the black bear as a result of the long relationship with the mother. I have included some notes on communication within the family group because communication appears important in training and survival. The combination of harsh discipline and indulgence is common in the training of young at many levels of animal organization, and female bears are competent in their application of this method. An additional benefit of family behaviour is heat conservation during the denning period when the mother and young "huddle" for warmth.

Females will defend their young against man on some occasions, and they defend them vigorously against other bears. Two things are apparent in this: survival of the young is enhanced when the family group endures longer, and other adults, apparently males, do kill or exclude young from the habitat. Wynne-Edwards (1962:529) accounts for the great difference in body size between male and female bears by placing the burden of population control on the male as a major secondary division of labour. His allusion apparently is to competition among the males during the breeding season, however, and not to the elimination of surplus young from the population.

This study has shown that black bear family groups, like other bear species, sometimes persist beyond the normal 1-1/2 years. The maternal instinct is therefore present during and after estrus, and this indicates that territoriality of the males causes the breaking up of family groups. The common belief has been that a change in the behaviour of the females disrupts the family, but it seems improbable that the female would suddenly become intolerant of the young after 1-1/2 years of constant care, then accept them back after she had been bred. The observation of a yearling nursing suggests that at high elevations where the season is shorter females sometimes nurse longer than normal. This could inhibit estrus two years consecutively, and because the female again skipped estrus, no males would join her. The family group would, therefore, remain intact another year, as some did during this study, and the reproductive rate would dip accordingly.

Female attachment to the young also leads to permanent social relationships in some cases. Several instances of young becoming established on their mothers' home range area were found in this study. This tolerance of related individuals by the resident female may have significance in population regulation through establishment of a social hierarchy in an area. This idea is supported by the way bears stay in very small home ranges that overlap with the ranges of a limited number of neighbouring bears. The establishment of such social groups that exclude other individuals could be based on learned familiarity among unrelated animals, or it could be a natural extension of family relationships. The observations of this study support this second premise, though it may not be exclusive.

Seasonal and daily changes in behaviour are also important in bear survival. During the breeding season males and females travel together, but at other times of the year bears under natural conditions are solitary. The flight of sub-adult males and of an adult female from adult males indicates that dominant individuals enforce this rule.

In the autumn bears have a reduced sensitivity to danger, and this too seems important in their survival. Their activity is reduced, conserving energy, and apparently family cooperation in the den is also augmented. Behaviour in the den includes the tendency to huddle, to curl the body, and to shiver, all of which are important in heat conservation or production. Kayser (1965) says that hibernators shiver only when aroused, whereas some bears in this study shivered continually while observed. During the denning period bears are able to fight or to move to another den, but they are seldom so inclined.

The dominance of feeding behaviour over other behaviour in the autumn probably contributes to their rapid build-up of fat stores. Black bears also shift their feeding behaviour from grasses and forbs in spring and early summer to berries during summer and fall, but this change is no doubt a result of reduced palatability of the grasses and forbs and the late development of the berries.

Through territoriality, many animals eject surplus young from a population, thereby effecting a regulation of population numbers. Another function of territorial behaviour is its action as a dispersion mechanism, reducing the density of animals in the most desirable habitats (Tinbergen, 1957). Social groups allow both these functions of territoriality, even under conditions of high density. Recently Carrick

(1963), Mykytowycz (1964), and others have shown that groups of individuals of a species exclude, either as a group or on an individual basis, other members of the same species.

Krott (1962) said that European brown bears are socially neutral animals, that they have no territories, and that "bear trees" are not marking places. Grinnell et al. (1937) said that both males and females mark trees and that this action is not to mark territory, but results from scratching and stretching, even though it takes on aspects of a ritual. Erickson (1965) says black bears are not territorial, since in Alaska they congregate on salmon streams and in Michigan they congregate on dumps. The evidence of this study is that bears have a form of territoriality, but that this behaviour is masked within social relationships with other bears in a given area. On a local scale, individual bears move about quite freely, but they are prevented by territorial pressure from moving only a few miles to an abundant food source, especially if the movement is lateral in elevation or downwards. The resultant small home areas keep the bears spread out in the permanent bear habitat at all times. Movements to high areas where food is temporarily abundant are not restricted. These high areas would probably be comparable to the "neutral areas" discussed by Hediger (1950:15). The evidence for territoriality among bears is, in summary, the high development and ritualization of agonistic behaviour; the circumstantial evidence of male participation in breaking up family groups and forcing the dispersal of young; the minimum overlap in the home ranges of adults of the same sex; the spacing of bears in distinct small home ranges despite the overlap of the ranges of mutually familiar animals; the marking of trees and other objects; the mutual distance kept by bears except during the breeding season; the inhibition of lateral movements by bears within good bear habitat; the freedom of movement of individuals into seasonally used areas; and the congregations in natural habitat only of bears resident in that area, bears adjacent to that area, or bears that have "learned" to break bonds or inhibitions and travel to a particular food source.

One could say the attachment to an area stems solely from the animal's desire to remain in familiar surroundings, but this alternative for explaining the sedentary nature of bears does not seem valid. Young males should also have this attachment, and my data have shown that they leave. Movements of certain bears outside of their home ranges and congregations of bears on salmon streams reported in other studies probably result when "learned" behaviour prevails over territorial behaviour, or it could mean territorial behaviour wanes during some seasons in the other areas.

Bears are polytypic in their behaviour with completely docile types that cower or seek concealment and very aggressive types that attack repeatedly when captured. These traits are no doubt important to different degrees in survival, but I found no way to measure this difference.

CHAPTER EIGHT

POPULATION CHARACTERISTICS AND REGULATORY MECHANISMS

Long-lived animals are suitable for the study of seasonal and yearly variations in the physiology or behaviour of individual animals, but they are not ideal subjects for the study of population phenomena because of the number of years involved. Since information on density, population structure, and growth of bears was essential for a study of both management and population regulation, however, I attempted to obtain these data. Also, population parameters of a species are important in comparisons between groups living in different forest or habitat types. These show the relationship between the performance of a species and its environmental conditions.

Density and Numbers

I estimated the population on the Big Creek study area by direct count and by the Peterson Index method using 1959, 1960, and 1961 data (Peterson, 1896). Since new animals in the population were added to the estimate as they were captured while the status of many animals not seen again was unknown, an adjustment for mortality was made. The loss from the population between 1959 and 1960 was calculated from the number of bears marked in 1959 that had disappeared through death or dispersal and that had not been observed or recaptured by 1965. As Table 9 shows, the estimate of the annual death rate becomes more accurate each year observations are continued; therefore the calculation based on 1959 is superior to an average of all years. Since data for other years were not as complete, the 1959 data were used throughout, even though death and dispersal rates do change from year to year. For example, in 1960 a high number of sub-adults were captured. The subsequent death and dispersal of the sub-adults apparently inflated the estimate of the death rate for that year.

The first estimate of density was based on a count of the total number of bears that had been tagged on the area during 1959 and 1960, plus the number of untagged bears estimated to be on the area but never captured. At the end of the 1960 trapping season 84 bears had been tagged, and only 12 of these were known to have been killed. In evaluating 100 observations of untagged bears during 1960, I estimated there were at least 18 untagged bears still on the Big Creek area. If the 1959 figures are adjusted for annual mortality, the total population in late 1960 was about 84 animals.

A similar estimate was obtained from calculations based on marked-unmarked ratios of animals observed during 1961 (Schnabel, 1938). This figure was also adjusted for winter mortality giving an estimate of 95 bears as the total population in 1961 (Table 10). A third calculation based only on capture and recapture data from 1961, and assuming that few bears became trap shy, gave an estimate of 104 bears (Table 10).

Year Marked	No. First Recaptured or seen again in Year Indicated							Minimum No. Surviving One Year or more after Marking	No. Gone or Dead	Annual Mortality
	1959	1960	1961	1962	1963	1964	1965			
1959	34	23	4	-	-	-	1	28	6	17.7
1960		65	32	4	5	2	1	44	21	32.3
1961			53	15	18	8	2	43	10	18.9
1962				32	18	10	3	31	1	3.1
1963					37	21	8	29	8	21.6
1964						44	34	34	10	22.7
1965							45	-	-	-
								Av.*		22.8

No. of old and new marked bears in year indicated

*Data for 1962 were omitted from the average because few new bears were marked that year. The data for that year, therefore, represents only the mortality rate of previously marked older bears living on the area.

Table 9. The numbers of marked bears of all ages on Big Creek at the end of each year and the number recaptured or observed in following years. The number known to have been killed through hunting or during handling was deducted from the total of old and new marked animals.

Type of Data	1961 Data - Obs. & Trapped		No. Marked 1959-1960 and at large			
	Total No. Bears (A)	No. Bears that were Tagged (C)	Unadjusted (B)	Adjusted (D)	AB	AD
Observations	53	29	72	52	3,816	2,756
Captures	47	23	72	52	3,384	2,444

Observations: $P = \left(\frac{AD}{C}\right) = \frac{2,756}{29} = 95$ bears (adjusted)

Captures: $P = \left(\frac{AD}{C}\right) = \frac{2,444}{23} = 104$ bears (adjusted)

Annual Mortality: Adjustment $= \frac{\text{1959 bears unaccounted for by 1955}}{\text{bears tagged - 1959}} \times 100$

$= \frac{6}{34} \times 100 = 17.7$ per cent*

*Adapted from Table 9.

Table 10. Estimates of the 1959-1961 Big Creek bear population from capture, observation, and recapture data. Adjustments were made for the calculated annual mortality. Bears known to be dead were not included.

The first estimate gave a density of one bear per 1.0 square miles during 1960; the second and third estimates placed the density in 1961 at one bear per 0.8 square miles. None of the three estimates took into account the possibility of higher mortality rates of marked animals, but Erickson (1959) showed that in young animals at least survival rates of injured and intact bears were almost equal. Also, the annual mortality rate no doubt includes some animals that merely emigrated.

An estimate of 48 bears on the area in 1966 was obtained in a similar manner from marked-unmarked ratios of bears observed in 1966 and was based on 47 marked bears known to be on the area in 1965. The estimate was adjusted for the 17.7 per cent annual mortality calculated for the bears marked in 1959. This low density of one bear per 1.7 square miles for 1966 indicates that the bear population had declined considerably from 1960 - 1961. Even though the density of bears was low in 1966, the increased percentage of sub-adults in that year indicates it was increasing.

Population Structure

I cannot describe the population structure of the Big Creek bear population adequately; far more detailed records of the population would be necessary. I do, however, have data on the marked animals that were killed and extensive data on animals still living on Big Creek. Also, I have partial records of a considerable number of the marked bears that have disappeared from the population through death or dispersal.

Table 11 shows that cubs (bears 4 - 9 months old) and yearlings (bears 16 - 21 months old) formed 29 per cent of 155 bears captured on Big Creek, a total almost identical with the results of Stickley (1961) in Virginia, but far below those of Erickson and Petrides (1964) in Michigan. Other sub-adults (bears 28 months to 4-1/2 years of age) made up a major portion of the Big Creek population, but there are no outside data with which to compare this figure. The percentage of adults in the population was higher during 1961, 1962, and 1963 (Table 12), but only because there were fewer sub-adults in the population. Most of the 47 bears killed on the study area were adults of both sexes (89 per cent).

The younger animals were not a stable part of the population. Table 13 shows that 20 per cent of the cubs remained in the population until two years of age, but only two sub-adult females remained in the population until 3-1/2 years old. One cub became a permanent resident on the area as she was still there in 1965 at 5-1/2 years of age. These numbers are low compared with the 60.4 per cent of the adults that remained three or more years and with the 10.4 per cent of the adults that remained in the population six to eight years. This topic was treated earlier in the section on death rates and in Figure 13.

Except for those shot by hunters, adult bears were long-lived once they became established members of the

Age Group	VIRGINIA No.	VIRGINIA %	MICHIGAN No.	MICHIGAN %	BIG CREEK Total of 155 Bears Captured No.	BIG CREEK Total of 155 Bears Captured %	BIG CREEK Total of 47 Known Dead No.	BIG CREEK Total of 47 Known Dead %
Cub	2	2	44	28	18	12	-	-
1-1/2	27	29	29	18	26	17	5	11
Total Cub & Yearling	29	31	73	46	44	29	5	11
Sub-Adult	-	-	-	-	47	30	10	21
Adult	-	-	-	-	64	41	32	68
Total Older Bears	65	69	85	54	111	71	42	89

Table 11. Age structure of the Big Creek bear population as compared with that found in other studies.

	Number of Marked Bears on Big Creek		
Year	Total	No. of Adults	Per Cent Adults
1959	37	17	45.9
1960	75	32	<u>42.7</u>
1961	63	35	55.6
1962	42	33	<u>76.2</u>
1963	46	29	63.0
1964	47	25	53.2
1965	49	23	46.9*

*This figure is low because it is based on data from only one year.

Table 12. The number and percentage of adults in the Big Creek bear population. The 1960 and 1962 data show the extremes in the numbers of adults present in the population.

		Alive 1 yr. Later		Alive 2 yrs. Later		Alive 3 yrs. Later		Alive 6-8 yrs. Later	
Age	No.	No.	% Surviving	No.	% Surv.	No.	% Surv.	No.	% Surv.
Cubs									
Marked	15	13	86.6	3	20.0	2	13.3	0	0.0
With marked Females	7	6	85.6	-	-	-	-	-	-
Total*	22	19	86.4	3	20.0	2	13.3	0	0.0
Yearlings	26	10	38.4	6	23.0	0	0.0	0	0.0
Sub-Adults (2-1/2 - 5-1/2)	31	15	48.3	12	38.7	7	22.6	2	6.5
Adults	48	36	75.0	33	68.8	29	60.4	5	10.4

*Only data on marked cubs were used after one year.

Table 13. The survival of individual bears tagged between June, 1959, and September, 1963. Only 1959-1963 data were used to allow sufficient time to determine if bears were present or not. Killed bears are not included in the table.

population. One female tagged as an adult in 1959 and one male tagged as an adult in 1960 were still on the study area in 1966. Four others tagged in 1959 and six tagged in 1960 were on the area in 1965 and are probably still there. The ages of the two seen in 1966 were unknown at the time of first capture, but both were at least 5-1/2 years old in 1959 according to their size and breeding condition. The female, therefore, was a minimum of 12-1/2 years of age, and the male a minimum of 11-1/2 years of age in 1966. Some bears on the study area are no doubt even older. A female from 10 miles southeast of the study area was 23 years old, as determined by the number of cemental rings in her lower canine (Stoneberg and Jonkel, 1966). Another bear killed on Lolo Creek in southwestern Montana had molars and premolars worn level with the gum line and had 24 rings in the cementum of an upper premolar, making her at least 23 years old.

Growth and Nutrition

It is hard to generalize about the development of wild animals since they have individual, seasonal, and sexual differences which vary with time and place and which have little relationship to the development of captive animals. It would be useful, however, in management and in understanding other population parameters if such easily measured characters as weight and rate of gain in weight could be used as an indication of nutrition and growth levels. I have tried to evaluate nutrition and growth levels for the Big Creek bear population and relate them to other population characteristics. The data are presented by grouping segments of the population.

Adult Females. The average weight of 76 adult females captured on the study area was 125 pounds, but those from higher elevations were significantly lighter than other females (Table 14). Weight differences were greatest when early spring and fall weights from one elevation were compared with early spring or fall weights of bears from other elevations.

Weights of adult females did not change much annually when they were weighed at the same time each year (Figure 14), but the weights of some individuals and the average weights of all adult females showed a slight decline during 1959 to 1965 (Figures 14 and 15). As shown in Figures 16 and 17, however, seasonal fluctuations in the weights of adult females were considerable. Weight changed little from early spring to early summer, but from then to denning time females gained rapidly (Figure 16). The great changes in the weight of selected individuals (Figure 17) illustrate the caution necessary when comparing bears from different areas if the time of the year is not noted. The most pronounced fluctuations were often related to the reproductive condition of the individual; for example both females No. 1 and 36 had cubs in 1961; No. 36 decreased from 140 pounds in the fall of 1959 to 88 pounds in June of 1960, while female No. 1 dropped from 200 pounds in August of 1959 to 116 pounds in July of 1960.

Adult Males. Adult males do not show a marked seasonal change in weight (Figure 14). They apparently endure the

	June		July		Aug.-Oct.		All Seasons		
Elevation	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	σ
4,400' +	17	112	8	118	15	138	41	122*	18
3,400_ 4,400'	14	120	7	120	11	147	35	128	23
Less than 4,000' (Outside of Big Creek)	-	-	-	-	-	-	5	184*	56

*No. 1 and 3 are significantly different at the 5 per cent level by Student's t test.

Table 14. The average weight in pounds of adult female bears captured at various elevations between 1959 and 1965 on Big Creek and in a ponderosa pine forest outside of the Big Creek drainage.

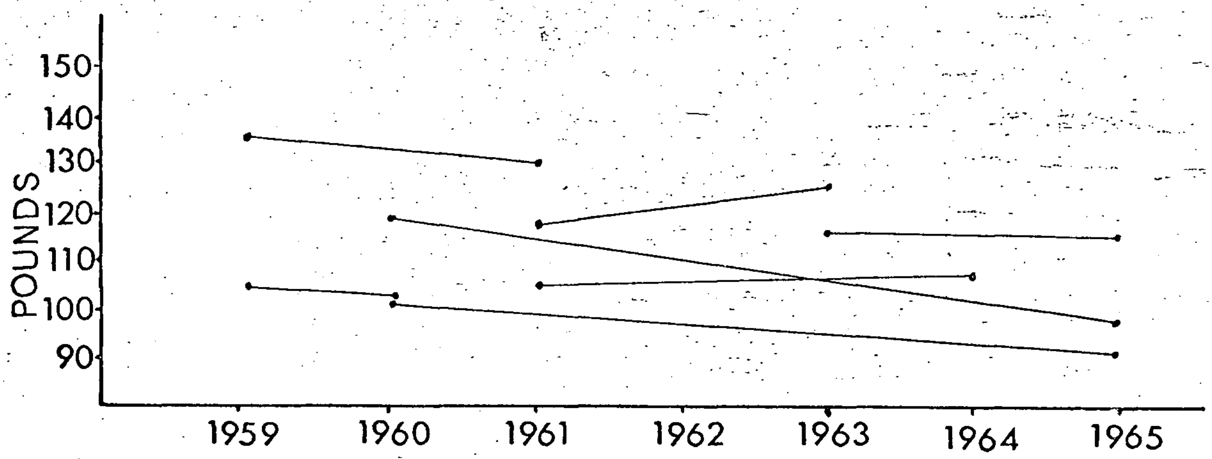

Figure 14. Individual weights of adult females captured in the same month in different years.

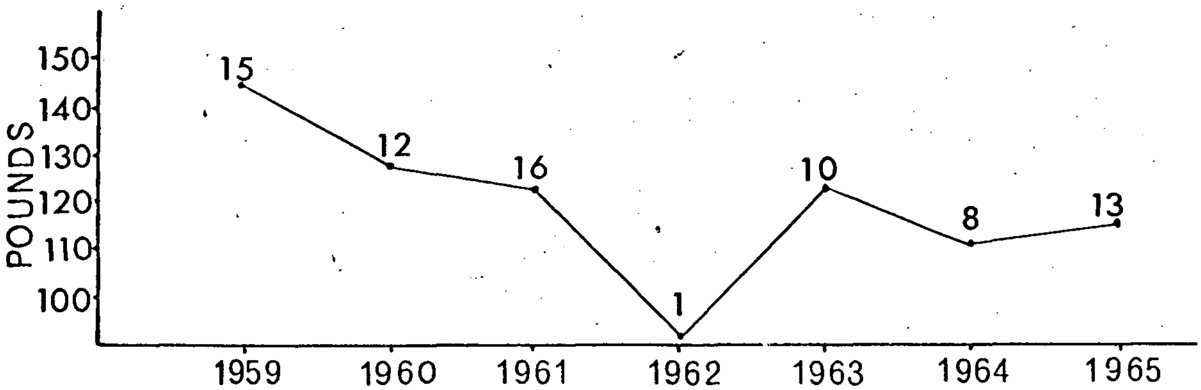

Figure 15. Average weights of adult females from 1959 through 1965. Numbers indicate sample size.

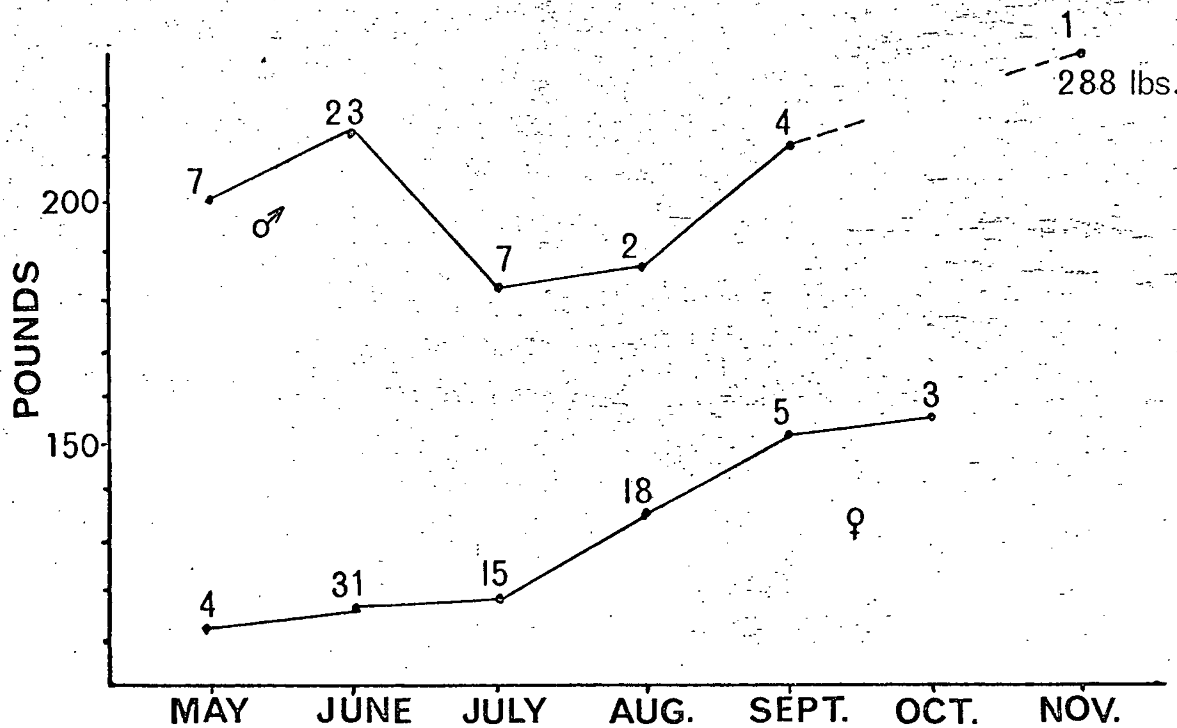

Figure 16. Seasonal growth of adult males and adult females. Numbers indicate sample size.

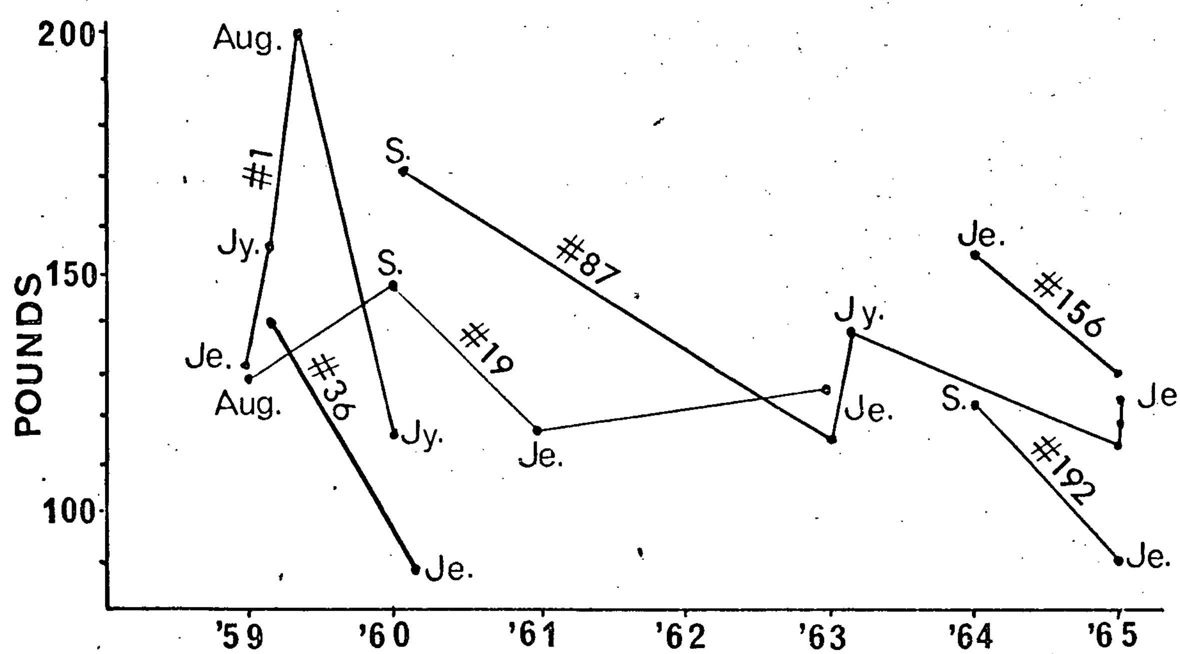

Figure 17. Weights of individual adult females at various times of the year. The numbers identify the individual bears and are discussed in the text.

winter denning period and early spring better than other bears and so have less weight to gain back each year. Adult males on Big Creek averaged 211 pounds during May and June, 188 pounds in July and August, and 225 pounds in September, October, and November. The differences were not significant by Student's t test. The weights of adult males did show a decline during 1961 to 1963 (Figure 18), which corresponds to the decline in adult female weights after 1959 (Figure 15), and is also correlated with the years of poor berry production on the study area (Table 15).

Unlike the females, individual adult males increase in weight annually for some years, even after sexual and physical maturity has been reached (Figure 19). Bears No. 50 and 62, for example, were at least 5-1/2 years old in 1960, but reached their maximum weights in 1964 and 1965. Bear No. 7 was 5-1/2 years of age in 1961, but increased to 260 pounds by 1965. These data tend to agree with those of Rausch (1960), who found that bone growth of captive bears continued until the sixth year, but that males increased in girth and total weight for several years thereafter.

Nine adult males captured above 4,400 feet averaged 202 pounds compared with 34 males captured between 3,400 and 4,400 feet that averaged 214 pounds. The difference was not significant by Student's t test. Unlike the more stationary females, the males moved to lower elevations during the spring and the breeding season, and only a small number of weights were recorded from higher elevations in the spring. Males are

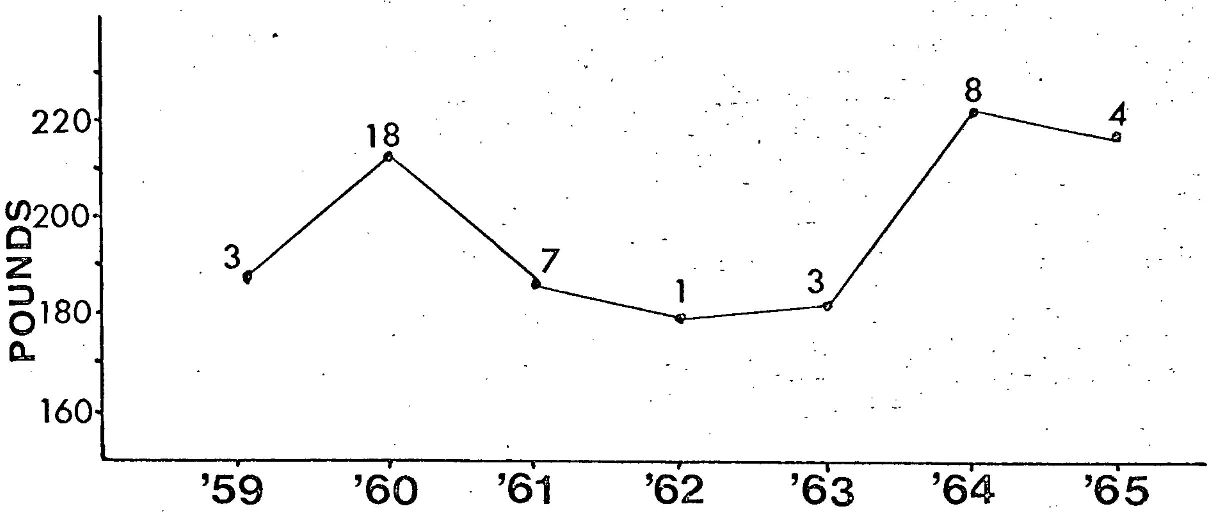

Figure 18. Average weights of adult males on the Big Creek study area. Numbers indicate the sample size.

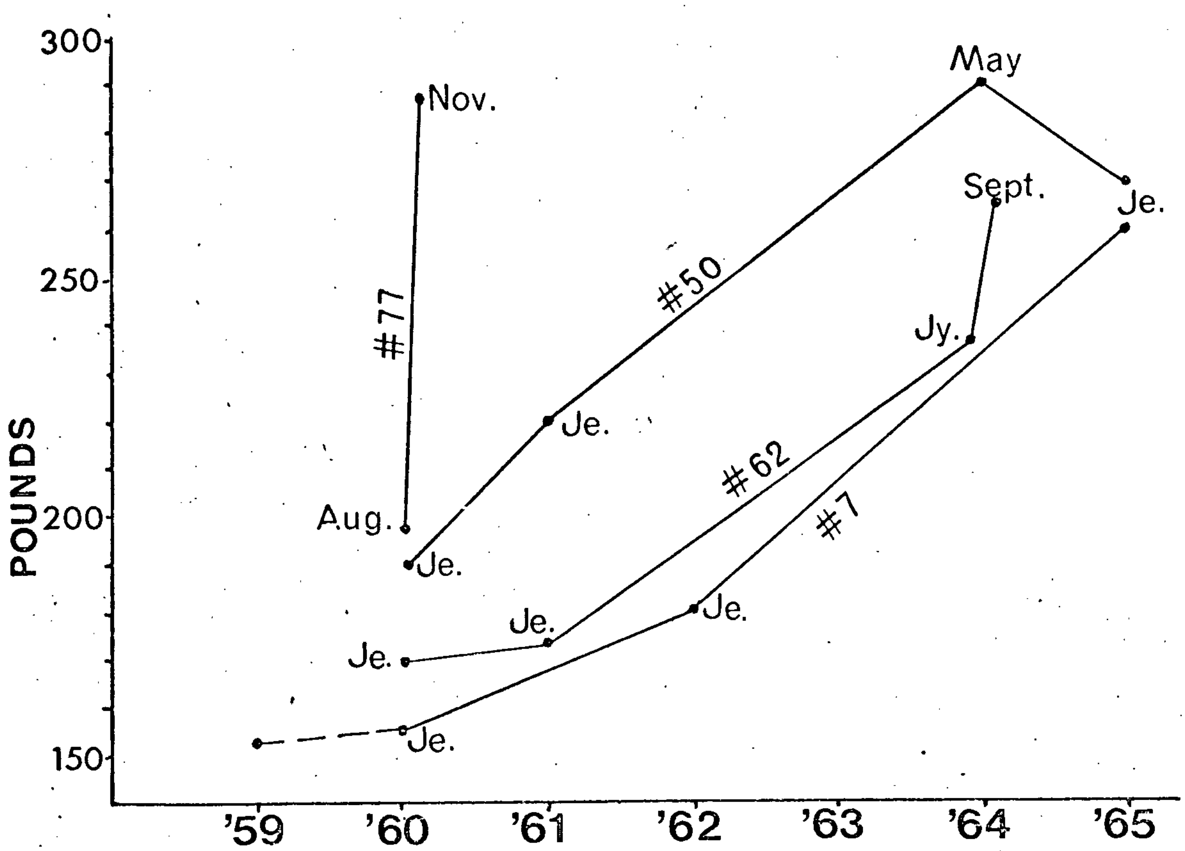

Figure 19. The weight of individual adult males on Big Creek.

Elevation in Feet	Relative Abundance of Huckleberries								
	1957	1958	1959	1960	1961	1962	1963	1964	1965
3,500-4,000	very abundant	common	few	abundant	few	few	abundant	few	very scarce
4,000-4,500	"	abundant	common	few	"	very scarce	"	"	"
4,500-5,000	"	"	few	"	"	"	"	"	few
5,000-6,000	"	"	"	"	"	"	"	"	"
6,000-7,000	"*	"	"	"	common	"	"	common	"

*Two feet of snow fell September 8.

Table 15. Huckleberry production on the Big Creek study area as determined by sample plots and annual estimates.

scattered widely throughout the extensive high country during the fall, making captures particularly difficult at that time.

Sub-adults. The weights of the sub-adults in the Big Creek study are a different matter. As shown in Figure 20, sub-adults increase in weight slowly in their first four summers, weighing only 60 pounds at 2-1/2 years. This slow rate of gain corresponds to their survival rates (see Figure 13).

In the wild there is very little difference in the appearance of a 45 pound yearling and a 60 pound 2-1/2 year old, but Figure 21 shows that within the study area the weights of young bears have a definite range for individual age classes when only the weights for each month are compared. There was no overlap within the first four age groups of bears from the Big Creek study area, but the weights of five cubs and two 2-1/2 year old bears captured off the area in the Douglas fir type completely overlapped with the weights of Big Creek bears 1-1/2 and 3-1/2 years of age.

The weights of 37 yearlings declined from a high of 49 pounds average in 1959-1961 (n = 25) to 27 pounds in 1963 (n = 3), but the weights of 1964-1965 bears showed some increase with an average of 38 pounds (n = 9). There was little difference in the weight of the two sexes in the first two summers, but 2-1/2 and 3-1/2 year old males were often heavier than females of the same age (Figure 20).

Rate of Gain. Bears of all age classes either gained weight slowly or lost weight during the spring and early summer. Bears foraged extensively during this period, and

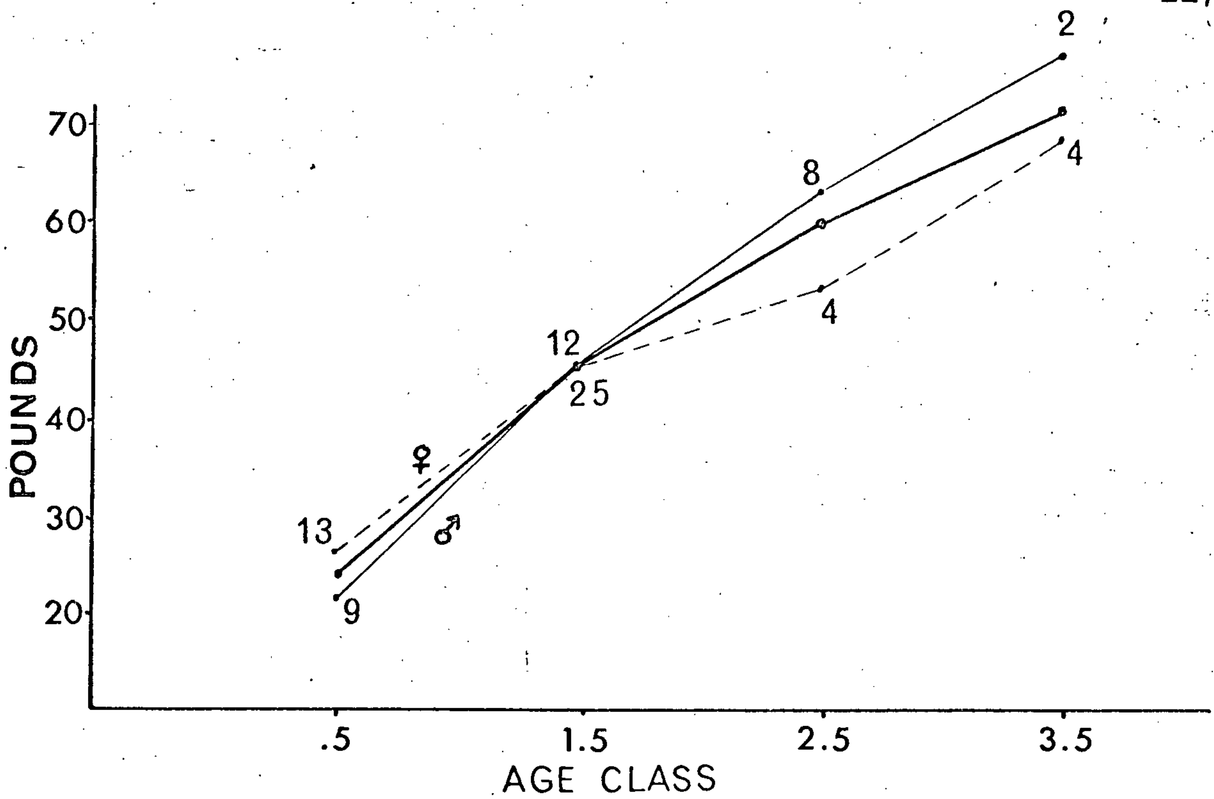

Figure 20. Average weights of known-age sub-adult bears on Big Creek. Numbers indicate sample size.

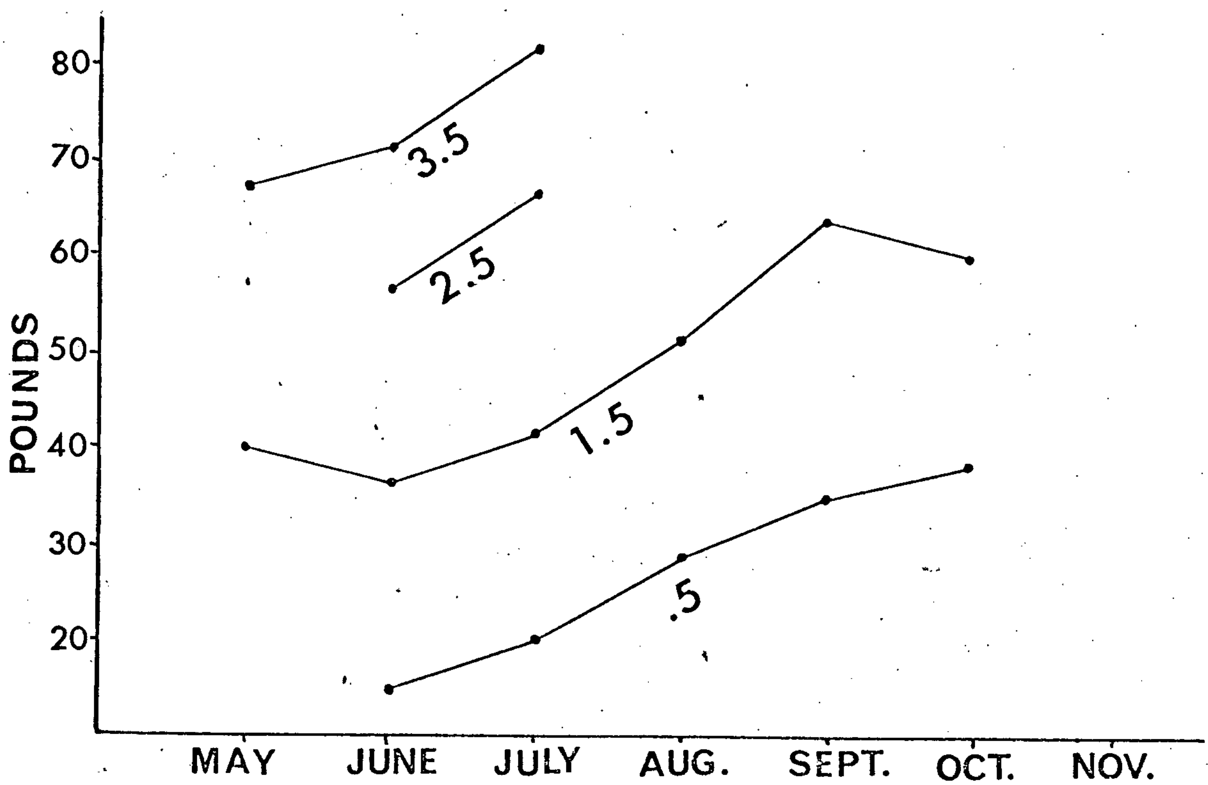

Figure 21. Seasonal changes in the average weights of known-age sub-adults on the Big Creek study area 1959-1965.

they ate a great variety of forbs and grasses (Tisch, 1961). However, 22 bears gained only 0.08 pounds per day over an average period of 21 days during this time (see Table 16 for individual rates). The greatest loss was 0.64 pounds per day over a 14 day period by a sub-adult female. Gerstell (1939) reports captive cubs gaining 0.208 pounds per day during early spring, and Erickson and Nellor (1964) said bears are lightest shortly after they leave the den in April; some bears in this study, however, reached their lowest weights in late June or early July.

The one exception when a Big Creek bear gained weight rapidly during this period illustrates the effect supplemental food can have in altering bear weight and development. This bear, a sub-adult female, fed at a construction camp in the centre of the study area during 1959 and gained 25 pounds in 30 days from June 6 to July 14. A more artificial case was a penned yearling male that grew from approximately 50 pounds in early spring to 185 pounds on September 24. This bear would have weighed about 60 pounds in September under wild conditions on Big Creek.

From mid-July until October all age classes of both sexes gained weight rapidly. In an average of 30 days, 14 bears gained 0.84 pounds per day, with one adult female gaining 1.55 pounds for 22 days (Table 17). Food during this season includes many kinds of fruits (Tisch, 1961). Black (1958) reported that in New York two bears with access to garbage gained an average of four pounds per day for three weeks during this same period.

Discussion

Population Characteristics. Changes in bear numbers have interested people for many years. Scott (1947) said that "bear populations fluctuate as do those of other game," and Schorger (1949) cited a number of alleged black bear irruptions in the early part of the nineteenth century in the upper Mississippi drainage. He concluded they were emigrations that resulted from the coincidence of acorn failure and a high bear population. Troyer and Hensel (1964) found that Kodiak bear population density in Alaska changed from year to year and that numbers were highest wherever food was abundant. Lawrence (in Black, 1958) reported a density of one bear per 0.25 square miles as measured in a bear removal project in Washington. This figure was no doubt augmented, however, by movement of sub-adult bears into the area as resident bears were killed. Using marked-unmarked ratios of bears killed by hunters, Erickson and Petrides (1964) calculated the population density at one bear per 3.4 square miles of bear range in Michigan.

Density of 1.0 bears per square mile in 1960 and one per 0.8 square mile in 1961 on Big Creek is high compared with that in Michigan. Comparisons of numbers from one area to another are incomplete, however, unless other components of the environment such as topography and timber type are also compared closely. For example, the 1960-1961 density for Big

Creek does not take into account that a significant, but unmeasured part of the 80 square mile study area is seldom used by the bears, as it is either outside the permanent bear range or in a stage of plant succession not used by the bears. Estimates of bear density from other studies may include larger unused areas of this kind.

The bear density on Big Creek declined to approximately one per two square miles through 1966. The ratio of adult to young animals on Big Creek those years also indicates the population had declined. Furthermore, the increased clear-cut logging in the area and the poor berry crops from 1961 to 1963 all lead one to expect such a decline. Density declined faster than expected, however, and unless clear-cut logging affects bears in some way other than through the amount of habitat lost, other causes for the decline must be involved. Certain bears avoided the area in which I was working just as certain of them became addicted to the trapsites. This could inflate the density estimates based on captures if other bears moved in, or deflate the estimates if they remained on their home ranges but avoided the trapsite area. I do not consider this an important variable in this study, however. There must be additional causes for the changes in bear density, and these causes will be discussed in the section on population regulation (p. 124).

Erickson and Petrides (1964) found that a Michigan series of 158 black bears was composed of 46 per cent cubs and yearlings, and Stickley (1961) listed 31 per cent of 94 black bears in Virginia in the same group. Troyer and Hensel (1964) reported that of 163 Kodiak bears (Ursus middendorffi) classified on Kodiak Island in Alaska, 48 per cent were in the cub and 1-1/2 year age groups, and they also reported that a survey of brown bears on the Alaskan Peninsula showed that cubs and yearlings made up 43 per cent of the population. The percentage of cubs and yearlings in the Big Creek population compares closely with the black bear population structure in Virginia, but is considerably lower than the percentage of that group in the Michigan population.

Some bias can be expected in any of the estimates, since those based on capture data are biased against females with cubs. The cubs restrict the movements of the females during part of the first year, and the females thus are not as prone to capture. Conversely, estimates based on observations alone are subject to chance distortion since family groups are more easily seen than single animals. Bias was kept at a minimum in this study by trapping intensively over a long period.

Most of the 47 bears killed on the area were adults, which agrees with the results of Troyer and Hensel (1964) showing that hunters usually select larger animals. Population structure based solely on bears killed by hunters is therefore less reliable. The Alaskan and Michigan bears are hunted more than those on Big Creek, and this probably explains the larger cub and yearling group observed in those populations. The Virginia population, which is similar to that of Big Creek in structure, is also hunted extensively, however, since Stickley (1961) reports that 33 per cent of the bears he tagged were shot the same fall. Yearlings and sub-adults are smaller on Big Creek than they are on other areas and are seldom shot. Perhaps Virginia hunters, by using dogs, kill greater numbers of the younger animals, even though they are small. The average weight that Stickley reports for adult males is low (157 pounds), which indicates he included many sub-adults in this group.

Average weights of adult females reported from other areas were 119 pounds in Virginia (Stickley, 1960), 149 pounds in Virginia (Stickley, 1957), 189 pounds in Florida, 183 pounds in New Hampshire, and 200 pounds in New York (Harlow, 1961:488). None of these weights was classified by season, but, except for the first set of data from Virginia, they were probably mostly fall weights. The adult female bears on Big Creek appear to be lighter than females from most other areas.

Adult male weights reported elsewhere are also heavier than those on Big Creek. Stickley (1960), however, reports adult males averaging 157 pounds in Virginia, and in an earlier paper (1957) he lists 375 males as averaging 175 pounds. These figures again must include considerable numbers of sub-adults, as he also reports males that weigh as high as 475 pounds. Harlow (1961:448) reports average adult male weights in Florida of 304 pounds, in New Hampshire 263 pounds, and in New York 324 pounds. These are mostly late fall weights. Bersing (1956) reports individual adult males of 400 to 500 pounds maximum in Wisconsin.

The weights reported for cubs in most other studies overlapped with the weights of yearlings and 2-1/2 year olds from Big Creek. Matson (1954) reported the weight of cubs in November at 70 to 90 pounds in Pennsylvania, and Knudsen (1961) listed cub weights in the fall at 95 pounds in Wisconsin. Beatty (in Schorger, 1949) reported a female cub in Yosemite Park, California, that weighed 80 pounds and a male cub that weighed 120 pounds at 10 months. Both animals had access to garbage. Black (1958) gave the average weight of five yearling males as 65 pounds and five yearling females as 74 pounds in New York, and Bersing (1956) reported the weight of two 1-1/2 year old animals as 102 pounds in Wisconsin. The only sub-adult weights from other studies that were similar to those of this study were yearling weights reported by Miller (1963) in Saskatchewan. He found that three yearlings of the brown phase weighed 25.0, 27.7, and 28.5 pounds.

Sub-adult bears on the Big Creek study area and in Saskatchewan are smaller, then, than bears of the same age in eastern North America. It may be significant that the brown phase makes up a major portion of the population in both the Big Creek area and Saskatchewan (see Appendix 2). Alternatively, however, the bears may be smaller as a result of a difference of food potential in these areas compared with eastern areas. Food can be important in this regard, since Rausch (1961) found that captive bears are physiologically older than wild bears, that they make more rapid growth, and that they become larger adults. This will be discussed further on page 131.

During the summer and autumn bears on Big Creek gained in weight rapidly in all types of habitat. Cowan *et al.* (1957) found an autumn change in the rate of gain for a captive bear, with a rate as high as 1.1 pounds per day at the start of the study, but as low as 0.06 per day later in the fall. They suggest this indicates a slowing of the metabolic processes, even in penned bears, as the denning period approaches. Apparently Big Creek bears do not reach the nutritional level necessary to slow the metabolic processes before denning in the fall, but they are less active during bad weather (unusually wet conditions either from snow or rain), and the rate of gain may thereby sometimes be slowed in the late fall. Most Big Creek bears fed until severe weather forced them to den, and at least one adult male continued to gain rapidly until early November in 1960. The weather was unusually mild that fall.

Two yearlings captured in February near the study area had weights normal for late autumn cubs, which suggests that weights are maintained well into the winter. I do not have a significant number of observations to permit an examination of weight loss through the winter months. Erickson (1961:300) reported a constant weight loss during winter in penned bears and said that, like woodchucks (*Marmota* spp.), they lose about 20 per cent of their weight.

Population Regulation. The topography and the climate of the Big Creek study area create good bear habitat and no doubt set ultimate limits to the numbers of animals that can live there, but they do not explain completely why numbers are neither more nor less at any given time. The number of bears killed from 1960 to 1963 on Big Creek by hunters accounts in part for the fewer cubs during 1961 to 1963 compared with those seen earlier or later, but not for the reduced number of cubs per adult female or for the lower density, since there were surplus sub-adults to counter this loss. Surrounding drainages were hunted very little.

Reproductive rates were high on the study area in 1959, and the large number of sub-adults present on the area at that time indicates that reproduction and the survival of young had also been high in previous years. Huckleberries were unusually abundant in the Whitefish Range for several years prior to and during 1959 (Table 15), and if food is in any way related to reproductive success in bears, these data correlate well, especially since during the following years of low huckleberry production all 34 adult females captured or observed on the study area were without cubs. Food supply would therefore be directly related to population control in bears. Correlations are not conclusive evidence, however, and other causes might be involved. Nonetheless, for bears it does seem appropriate to search for external causes of variations in reproductive rates and survival of young, since the same adults are on the area from year to year.

Dispersal of sub-adults from the area was common and involved mainly the males. Dispersal of young animals from any stable population can be expected, but dispersal becomes far more likely if the members of the population are territorial (Errington, 1956). Two of the dispersing sub-adults in this study were recaptured in extensively farmed areas of the Flathead Valley, an area not considered good bear habitat, the implication is that they were somehow forced to search for range outside the normal bear habitat. These results agree in part with the statement of Margelef (1963) that young animals are forced into marginal habitat or areas of seral vegetation, while the adults remain in the climax forest to which the species is adapted. Dispersal of young males is a permanent drain on the Big Creek population since much of the movement is into areas of poor bear habitat where some bears are shot and others probably die from other reasons at a faster rate. I could not determine if this dispersal rate is constant or if it changes under different levels of density or with food shortages.

The causes of natural mortality and their role in population regulation remain obscure, but mortality rates for cubs and adults were so low they can be disregarded in annual density changes. After 1-1/2 years of age, however, bears rapidly disappeared from the population. The stable adult population (41 per cent on Big Creek) is thereby left in control of the habitat. Once bears become adults, the death rate, other than that caused by hunting, is quite low. In zoos bears have been known to live to 20 - 30 years of age, and this study shows some bears do live that long in the wild. Even some of the annual 14.0 per cent adult mortality measured was no doubt caused by poaching or uncooperative hunters. The actual natural death rate for adults is probably between the five per cent natural mortality rate for the young from 1/2 to 1-1/2 years of age and the 14.0 per cent annual mortality measured for adults. Any large annual fluctuations in natural populations, therefore, must occur as changes in the rates of follicle maturation (total numbers), prenatal mortality, or deaths of animals in the older sub-adult group. Consumption of hormone-like substances in plants (see Appendix 3), nutritionally or genetically controlled differences in size, and yearly differences in food supply may all be involved. The last two deserve additional comment.

Rausch (1961) has shown that penned black bears mature sexually and physically much sooner than wild bears. Potentially, with good nutrition, bears have litters every other year; some bears on Big Creek did, but others skipped two and three years. Theoretically, 50 per cent of the adult females should have young each year, but some force drastically reduced the realization of this potential. Although the quality of the bear habitat on Big Creek allows a high population density, the short annual growing season causes bears to mature more slowly sexually and physically. Females are not successful in reproduction until 5-1/2 - 7-1/2 years of age. This short season even restricts the adults nutritionally, especially in certain years. Studies on other animals have shown that poor nutrition can affect prenatal and earlier reproductive failure. With my data, the assumption could be extended to bears, which supports the conclusions of Rausch (1961) for penned bears. Part of this restriction in the food supply can act secondarily on the female through the nutrition of the young. Smaller yearlings at high elevations sometimes suckle up to 16 months of age, and this stimulus may be inhibiting estrus for two consecutive years.

Mortality rates for sub-adults apparently change annually in response to changes in food supply. Younger sub-adults are in poor condition in late spring as a result of the energy lost during the denning period and because of increased energy demands as they feed during late April, May, and June. The food apparently is poor for bears during this time, and the sub-adults in particular lost weight rapidly. I have handled some bears 2-1/2 to 3-1/2 years of age in May and June that were so thin and weak they did not need to be drugged. In that condition they must be vulnerable to climatic changes and a number of other decimating factors, any of which could change annually. This loss in weight is not under endocrine control since bears that had access to garbage or were fed during this same period gained weight rapidly. Erickson (1961:200), too, found that penned bears regained their weight rapidly in the spring.

Other forces that limit density, though less likely to affect populations annually, are differences in behaviour and genetic composition. This study was begun with the assumption that population regulation was largely through extrinsic factors, and the problem undertaken was to determine what those limiting forces were. As shown in the sections on mortality and behaviour in this paper, it now appears that both extrinsic and intrinsic causes work together in regulating the Big Creek bear population annually and over long periods. The major causes involved in annual fluctuations seem quite different from those involved in long-term regulation of population density. The annual causes of population change seem centred on reproductive failure and loss in the sub-adult group. These causes appear to be a combination of extrinsic and intrinsic forces; poor nutrition, the primary extrinsic force, and male antagonism, probably the most important intrinsic force. Male antagonism apparently helps break up family groups, results in some cannibalism, and forces dispersal of young, setting the stage for other controls.

Habitat is important in determining bear density, but the bears on Big Creek also have reproductive and behavioural characteristics that are unique in maintaining long-term population levels. These characteristics may be evolutionary adaptations to the spruce forest of the West, since bears on Big Creek and throughout Montana have smaller litters than eastern bears. Apparently this lower average litter size is not an indication of an unexploited population nor would the average change if more bears were killed, since the litter size was constant throughout the state and from year to year. Also corpora lutea and mature follicle counts from Montana and Washington bears were the same as the litter counts, and litter sizes reported for Alaskan black bears by Erickson and Nellor (1964) were comparable with those of Big Creek bears rather than with those of Eastern bears. A longer breeding season might also be an adaptation of bears in this area, but possibly the length of the breeding season has not been measured adequately elsewhere.

Bears living in an area like Big Creek must come into contact with each other far more often than bears dispersed on large home ranges. Social behaviour is more developed in this case, and what this might mean in terms of reproduction or stress is unmeasured. Albrecht _et al_. (1959) have shown in the locust that crowding of larval instars increases the number of egg pods laid by ensuing adults, but this is opposed by an inhibition of egg laying when the adults are crowded. It is also commonly held that high density adversely affects mammalian and avian populations by increasing mortality rates, especially among the offspring (Cheatum and Severinghaus, 1950; Tanner, 1966; Perrins, 1965).

Under natural conditions black bears do not form large groups like herbivorous animals or even the several generation family groups common to grizzly bears. Family groups do sometimes remain intact for about two years, but, more significantly, the bears in a given area have a social order which apparently allows them to share a minimum range while a form of territoriality still functions to regulate population density. My data are not complete, but bears resident in an area tend to exclude non-resident bears while they tolerate bears with whom they are familiar, thereby maintaining continually a higher population density on Big Creek. This familiarity stems at least in part from earlier family relationships, and may even extend to adults of the same sex, at least among females. Contrary evidence of bears moving long distances to garbage dumps or salmon streams through the ranges of strange bears could be explained by learned behaviour or cultural inheritance. Comparative data from other areas could clarify this point.

If, as my data indicate, there is survival value in the colour of bears (see Appendix 2), this may be further evidence that climate is involved in the nutrition and population dynamics of bears, and thereby accounts for the distribution of the brown phase in North America. The peculiar continental distribution of the colour phases of black bears and the occurrence of the various phases within family groups denotes a genetic cause. The relatively high occurrence of the brown phase in the central Rocky Mountain area, surrounded by almost entirely black populations along the west coast, in the Arctic, and throughout eastern and southeastern North America, indicates that the brown phenotype is somehow favoured in the central area. The ample opportunity for gene flow in the Minnesota-Manitoba and Northwest coast areas probably rules out isolation.

The concluding implications of my population studies on black bears are that because of varied vegetational and topographical conditions, Big Creek is excellent habitat for adult bears, but because of climatic extremes, high bear density, and other shortcomings, it is an hostile environment for sub-adults. Annual changes in birth rates and in the survival of sub-adults cause annual changes in population density. Though the habitat, and to some degree behaviour, allow a density higher than those in eastern North American areas, Big Creek bears do have behavioural and genetic adaptations that reduce the size and frequency of litters. These, along with nutrition, set long-term population levels. Countering this, the survival rates of individual young are increased because of the small litter sizes and because the young receive care from their mothers for longer periods. This care apparently extends to the establishment of a strict social hierarchy in local areas, allowing a greater density in a basically territorial species.

PART III

CONCLUDING REMARKS

CHAPTER NINE

CONCLUSIONS AND SUMMARY

1. The multitude of different exposures and slopes throughout Big Creek provides a patchwork of habitat that ranges from desert-like conditions to permanent snow fields. There were two major types of bear habitat on Big Creek; areas that were heavily forested and lower in elevation, and areas that were thinly forested, high in elevation, and free of snow only during summer and fall. Bears had permanent home ranges in the forested lower type, and most bears did not move into other portions of this type under any circumstances, except dispersal. The seasonally used areas did not support bears permanently, but when food was abundant there, bears from adjacent areas moved to it freely.

2. The _Picea_-_Abies_/_Pachistima_ association was an important component of bear habitat during all seasons. Other types of habitat were important seasonally: dry meadow areas in early spring, snowslides and stream bottoms in early and mid-summer, and the _Picea_-_Abies_/_Menziesia_ and _Picea_-_Abies_/_Xerophylum_ associations in the fall. Clear-cut logged areas were avoided.

3. Home ranges of Big Creek bears were very small compared with those elsewhere. Greatest movements averaged 1.6 miles for adult females and 3.9 for adult males. Home range estimates

based on measured movements were considered best for Big Creek bears because of the linearity of the habitat and the extremes of elevation on the study area. Ranges of adults of the same sex overlapped only occasionally, but sub-adult ranges usually coincided with adult female ranges. The ranges of one sub-adult male increased as he matured, perhaps because an adjacent male was killed.

4. There were no "migrations" of bears, but bears did congregate on slides or dry meadow areas when such an area was shared in their ranges. Bears also moved readily within their home ranges to the food on seeded strips along logging roads.

5. Bears on Big Creek denned an average of 1-1/2 months longer than bears reported elsewhere. Winter comes early and is severe, and all bears den regardless of their nutritional state. They seem to be well adapted, however, to survive even this longer period. Some of their behaviour such as curling and den building is similar to that of true hibernators, but most of the denning behaviour observed during this study indicates that winter is rather like an extended waiting period for the bears. They are easily aroused by any approach to the den and are often quite active in the den when under observation.

6. Dispersal of sub-adults was common and involved mostly males. No estimate of the true magnitude of this dispersal from the area was made, but 13 movements were recorded. Territoriality imposed by the adult males seemed to be involved,

but dispersal rates may increase with food shortages.

7. The sex ratio of the total bears captured on Big Creek was even, as were the sex ratios for the cub and adult age groups. Bears 1-1/2 or 2-1/2 years of age and other unclassified sub-adults deviated significantly from an even sex ratio, probably because many sub-adult males moved through the area.

8. Females on Big Creek were in estrus from late May to early August, with a peak from mid-June to mid-July. Male-female pairs were observed only during June and July, five females from Washington had mature follicles between June 9 and June 27, and one female from Washington had corpora lutea on June 14.

9. No bears younger than 4-1/2 years of age were observed in estrus on Big Creek, and none of those observed was successful in raising litters before 6-1/2 to 7-1/2 years of age.

10. The average litter size on Big Creek was 1.7 and for all of Montana it was 1.6. The average number of corpora lutea and mature follicles was 1.8 for Big Creek and 1.9 for Washington bears. Yearling litter sizes on Big Creek averaged 1.6. These averages are low compared with litter counts of 2.2 to 2.6 and corpora lutea counts of 2.4 for bears in eastern North America.

11. Potentially, bears can have litters every other year; some bears on Big Creek did have young that often, but some skipped two years and two skipped three years. Only 16 per cent of 96 adult females examined had litters. In 1959 and 1964 almost 50 per cent had litters, but from 1961 through

1963 no marked females had young, although a few unmarked females on the area did have cubs those years. Reproductive rates declined when the abundance of huckleberries declined, and increased when huckleberry production increased, but this may be a mere correlation.

12. Hunters killed three per cent of the bears tagged in 1959, but by 1961 the kill increased to 10 per cent of the animals marked that year. Some of the forces involved in natural population control remain obscure, however.

13. Little evidence of the causes of prenatal or early mortality was found. Ultimate causes appear related to the small size of the females, consumption of estrogen-like substances in plants, or genetically controlled behaviour. Bioassays showed that cow parsnip, which some bears eat in the spring, is powerfully anti-estrogenic. The potential for delaying or inhibiting the maturation of follicles is obvious. Similarly, whitebark pine nuts have an estrogen-like action that could terminate pregnancy in the fall.(Appendix 3).

14. Cub and adult mortality rates were low and no natural mortality was observed. Older sub-adults disappeared rapidly from the population, but part of this loss was from dispersal. Annual variations in sub-adult mortality rates from extrinsic factors are quite probable since many bears of that age group are in extremely poor condition in late spring. No mortality during the denning period was recorded for 31 bears.

15. Internal and external parasites were found in Big Creek bears, but only ticks were abundant. No diseased animals

were found. Predation by adult black and grizzly bears on small black bears was recorded in Big Creek and vicinity, but the incidence was low.

16. Climate influences nutrition by extending the denning period and by creating annual fluctuations in food quality. Climate seems thus indirectly involved in mortality.

17. Agonistic behaviour in black bears is more highly developed than was formerly recognized, and family behavioural relationships are elaborate. The family group also benefits from cooperation during the denning period. Females sometimes defend the young against man and against adult males.

18. Family relationships usually endure 1-1/2 years and then break up in late June. My observations suggest that during the breeding season the male disrupts the family group through aggression towards the young. Some family groups may endure longer than normal at high elevations because females skip the estrous cycle two years. Some family relationships result in permanent associations.

19. Seasonal changes in behaviour influence dispersion of bear populations. Males and females travel side by side during the breeding season, but the rest of the year bears keep a mutual distance of 50 yards or more.

20. Bears have a reduced sensitivity to danger from autumn through winter. This aids in survival, since they are not easily frightened away from the protected area of their den.

21. Territorial behaviour in bears is strongly indicated by this study, though it is masked by "social groups" of bears

that tolerate each other, but exclude other bears. Contrary evidence of bears moving long distances to garbage dumps or salmon streams might be explained by learned behaviour.

22. Individual variation in behaviour is great, ranging from docile to very aggressive types. Survival rates may be affected by these differences.

23. The density estimates of approximately one bear per square mile on the Big Creek study area were high compared with estimates from elsewhere. The density on Big Creek declined from 1960 to 1966, but recovery was noted during 1965 and 1966 as reproductive rates increased.

24. Cub survival was high from 1/2 to 1-1/2 years of age, but the young then rapidly disappear from the population through death and dispersal. Adults are stable in the population because their survival rate is high, and they do not disperse from the area.

25. Adult females from high elevations on Big Creek were lighter in weight than those from lower elevations, and individuals showed a great seasonal change in weight. Sub-adults on Big Creek were smaller than bears of the same age elsewhere, probably because they had poor food for a longer period in the spring. A genetic cause cannot yet be ruled out, however, since small size could be related to the colour of bears.

26. The weights of the sub-adults were distinct in their range if care was taken to compare only the weights of animals captured during the same month of the year.

27. During April to early July most bears lost weight or only just maintained their weight, but from mid-July until they denned they gained up to 1.5 pounds per day. On Big Creek inclement weather probably slows the rate of gain near denning time, but bears did not cease feeding as has been reported elsewhere.

28. The brown phase makes up one-third of the Big Creek population, and brown bears are found throughout the central Rocky Mountain region. Colour is no doubt controlled genetically in the black bear, but the mechanism remains obscure.

29. Annual changes in population density are correlated with a decline in average weights of bears; a lower ratio of adult to young animals, a virtual absence of reproduction during 1961-1963, increased hunting pressure through 1963, increased logging activity, and poor berry crops from 1961-1963. Trapping operations may also have curtailed the population density slightly. The number of sub-adults in the population declined as density declined, but the number of adults did not vary significantly during the study, primarily because adult bears are long-lived, are strongly attached to their home range area, and have a low annual mortality rate.

30. Long-term control of population density seems dependent on the habitat of Big Creek and on unique reproductive and behavioural characteristics of the bears resident there. Conditions seem exceptionally favourable for adult bears, but weaned sub-adults lead a precarious existence and often perish.

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APPENDIX 1

Bear No.	Sex	First Capture Date	First Capture Weight (lbs.)	Second Capture Date	Second Capture Weight (lbs.)	Loss or Gain (lbs.)	No. of Days
174	M	6-19-64	13	6-30-64	15	+2	11
56	M	6-4-60	42	6-29-60	40	-2	22
160	M	6-26-64	55	7-1-64	52	-3	5
170	M	6-4-64	38	6-15-64	37	-1	11
163	M	6-28-64	53	7-16-64	66	+13	18
172	M	6-15-64	39	7-9-64	46	+7	24
169	F	6-4-64	52	6-29-64	51	-1	25
170	M	6-8-65	80	7-16-65	91	+11	38
61	F	5-27-63	65	5-31-63	69	+4	4
157	M	6-7-65	72	7-13-65	82	+10	36
31	M	6-30-60	56	7-7-60	56	0	7
10	F	6-4-60	103	7-21-60	92	-11	47
48	F	5-21-60	52	6-5-60	52	0	13
51	F	5-22-60	107	6-5-60	98	-9	14
203	M	6-27-65	62	7-13-65	65	+3	16
168	F	6-4-64	67	6-12-64	65	-2	8
49	M	5-22-60	195	7-7-60	187	-8	47
50	M	5-22-60	190	6-20-60	190	0	29
62	M	6-28-61	173	7-25-61	175	+2	27
162	F	6-23-65	114	7-9-65	120	+6	16
87	F	6-4-65	115	6-23-65	125	+10	19
50	M	6-5-65	263	6-26-65	270	+7	21

Table 16. Gain or loss in weight for 22 bears over various periods during the spring.

Bear No.	Sex	First Capture Date	First Capture Weight (lbs.)	Second Capture Date	Second Capture Weight (lbs.)	Gain (lbs.)	No. of Days
17	F	8-7-59	25	8-25-59	42	+17	18
18	F	8-7-59	25	8-22-59	35	+10	15
72	F	7-20-60	18	8-20-60	22	+4	30
69	F	7-19-60	41	8-4-60	44	+3	14
120	F	7-13-61	49	8-7-61	59	+10	25
8	M	7-25-59	40	8-26-59	58	+18	31
18	F	8-7-61	73	8-18-61	80	+7	11
2	F	7-21-60	103	9-12-60	170	+67	53
1	F	7-14-59	155	8-26-59	200	+45	40
23	F	8-11-59	141	8-27-59	152	+11	16
75	F	7-13-61	114	8-4-61	148	+34	22
75	F	8-4-61	148	8-7-61	151	+3	3
77	M	8-4-60	198	11-6-60	288	+90	94
62	M	7-10-64	235	9-4-64	265	+30	45

Table 17. Gain in weight of 14 bears during late summer and autumn.

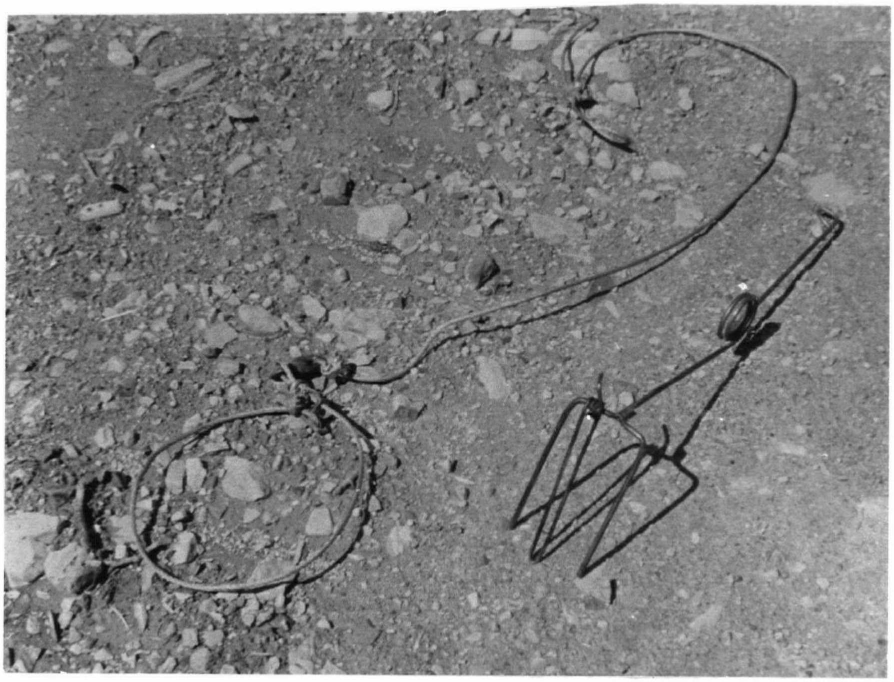

Figure 22. Aldrich trap and snare.

Figure 23. Newhouse 150 steel trap, canvas for weighing bears, and a recovering black bear.

Figure 24. Cubby type trapsite showing stepping sticks.

Figure 25. Closed forest type.

Figure 26. Open forest type.

Figure 27. Snowslide through a mature spruce-fir forest.

Figure 28. Dry meadow type in the spruce-fir forest.

Figure 29. Seeded strip along the Big Creek road.

APPENDIX 2

COLOUR PHASE

The black bear is one of several North American species known for the existence of different colour phases in the population. The relative abundance of the several phases differs in a broad regional pattern throughout the range (Cowan, 1938). Nothing is known of the genetics of colour phase in the black bear, but the occurrence of the light brown phase as an abundant element throughout the Central Rocky Mountain area over a period of more than a century suggests a selective force functioning to maintain a balanced polymorphism. Speculation on the possible genetic mechanisms in force are beyond the scope of the present study, but some of my observations suggest a possible mechanism whereby the brown phase may experience at least periodic and local selective advantages.

On Big Creek 32.3 per cent of 158 bears were brown, and 8.2 per cent of these were of the light brown phase. All light brown bears (five) were females. Of 75 cubs and yearlings examined, 44.0 per cent were brown, while 31.2 per cent of 77 adults were brown. Females of the black phase had mostly black cubs (80.0 per cent), while brown females had mostly brown cubs (86.2 per cent); each had a low incidence of mixed litters (Tables 18 and 19).

Female		Litters of Cubs and Yearlings		
Colour	No.	Black	Brown	Mixed
Black	29	22	4	3
Brown	16	1	13	2
Total	45	(23)	(17)	(5)

Table 18. The colour of female bears and the colour composition of litters.

Animal	Black	Brown	Light Brown
Cubs and Yearlings			
Black Mother	36	9	0
Brown Mother	3	19	5
Total	(39)	(28)	(5)
All Sub-adults	54	20	7
All Adults	53	19	5
Total (all bears)	(107)	(39)	(12)

Table 19. Colour phases of bears captured on the Big Creek study area.

A review of the literature and a survey mailed to Game Departments showed that the brown phase is common in black bears from central British Columbia and Alberta south to Colorado and California (Figure 30). The central Rocky Mountain area harbours the greatest numbers of brown bears, but they are abundant in the Sierra Nevadas in California and in the Cascade Mountains in southern Washington (Black, 1958; Hamilton, 1943; Elliot, 1901; Cowan, 1938; A. W. Erikson, R. F. Harlow, and L. E. Brunnett, personal communication). The bears in this area are often considered to be of the subspecies *U. a. cinnamomum*. Arizona and Texas have too few bears left today to determine any ratios.

The brown phase seems most common along a line running from central California to Saskatchewan (Grinnell *et al*., 1937; Cowan, 1938; Miller, 1963; C. E. Kebbe, personal communication). Pierson (1964) reported that of 517 bears trapped in western Washington in 1964, 31 per cent of those taken in the Mt. St. Helens area were brown, while those taken on the Olympic Peninsula 100 miles northwest were all black.

In many species colour is related to differential predation or to sexual behaviour. Gloger's Rule states that in some species colour is an adaptation to climatic conditions. Colour in bears was investigated to test whether the survival of different coloured animals was related to the environment, and if they were related, in what way. Natural mortality in bears seems highest in the sub-adult group in spring when they are in poor physical condition and are feeding on the

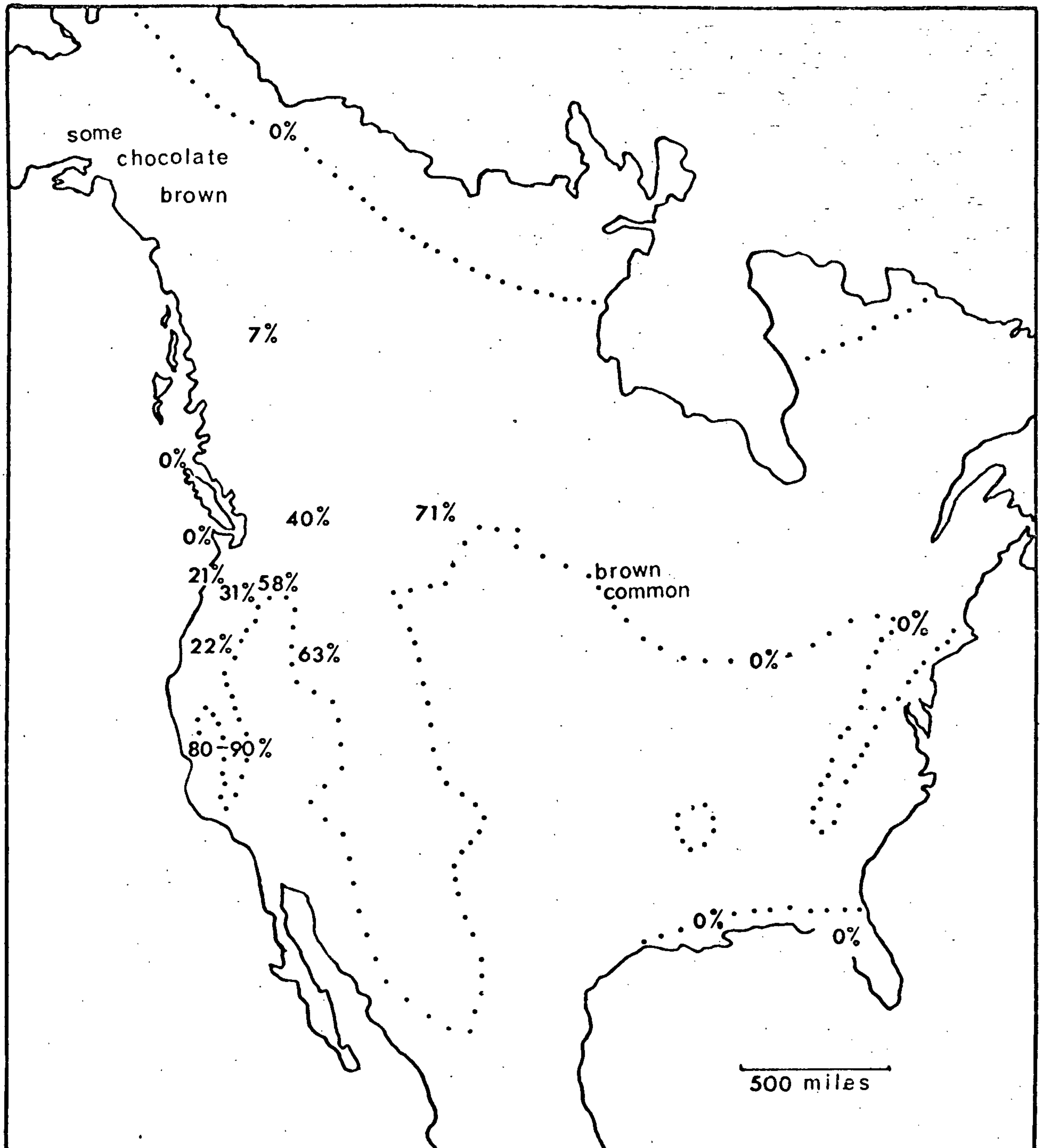

Figure 30. The distribution of the brown phase in black bears. Distribution of the species is based on A Field Guide to the Mammals. W. H. Burt and R. P. Grossenheider. 1964. Houghton Mifflin Co., Boston xxiii + 284 pp.

open dry meadow areas. It seemed possible, therefore, that if colour was related in some way to capacity to obtain food during this period, there could be a selective mechanism operating. Accordingly, I have assembled the observations referring to colour phase and the length of time spent feeding in the choice exposed areas. Observations were made on 276 bears primarily during May and June. The results were as follows:

	No. of Bears Observed			Percentage Brown	
Time	Total	Black	Brown	Expected	Actual
1:00 A.M. to 8:00 A.M. and 5:00 P.M. to 10:00 P.M.	150	110	40	32.3	26.7
8:00 A.M. to 5:00 P.M.	126	72	54	32.3	42.8

Expected values were based on the colour of 158 bears captured on Big Creek and on the assumption brown bears and black bears have an equal probability of being captured. The number of brown bears observed during mornings and evenings did not deviate significantly from the expected, but during midday (8:00 A.M. to 5:00 P.M.) the number of brown bears observed was higher than expected (five per cent level of significance using the Chi-square test).

Hingston (1933) says bears can be an obvious colour such as black because they have little to fear. Inherent in this is the implication that brown phases would be selected for under heavy predation. Information on predation on bears is scanty, but as I noted earlier, both adult black bears and grizzly bears are predators on small black bears. Lewis and Clark in 1804 and 1805 saw few black bears in the grizzly country between the little Missouri River in North Dakota and the Columbia River (Burroughs, 1961) where they are now common, and this implies that predation might have been significant in the past. Brown bears are harder to see on open hillsides, suggesting the reverse of the well-known phenomena of industrial melanism in moths, but whether this would be protection against a predatory grizzly, an adult black bear, or man is another matter, especially since bears apparently use scent more than vision in their hunting.

A possible alternate explanation for the maintenance of the brown phase in this region concurs in part with Gloger's Rule. On a continental scale, most of this area lies within what is known as the Great American Desert. Despite the rain forest conditions existing within my area (see Chapter 2), those habitats most critical to bears in spring and early summer are in effect "desert" areas. By mid-June the vegetation on these exposed areas has flowered, fruited, and completed its growth. These openings are especially important to sub-adult animals, which are in extremely poor physical condition at that time of the year following the rigours of winter and the heavy tick infestations. They apparently have difficulty obtaining adequate nutrients from the forbs, sedges, and grasses, and they either lose or barely maintain their weight. Under these conditions, the length of time they can feed each day could become critical. As I noted earlier, during spring bears of the brown phase feed over a longer period on the open areas which produce more food. By feeding longer in each 24 hour period, they thereby could be selected for during spring. Seven sub-adults of the brown phase did gain an average of three pounds, while nine of the black phase gained no weight during a three week period in the spring, but the differences were not statistically significant. It has been shown for other species (Gershenson, 1945) that there can be differential survival of colour phases of mammals, and Hamilton and Heppner (1967) found that the absorption of radiant solar energy increased greatly when they dyed black the feathers of white Zebra Finches (*Poephila castanotis*).

Dowdeswell (1955) says the selective advantage in polymorphic species can be up to 30 per cent and describes a change in form of the meadow brown butterfly (*Maniola jurtina*) in one year when grazing by cattle was discontinued in an area. Sheppard (1960) and others have pointed out that genetic properties can seldom be neutral in their effect for more than a short period of time. Whatever the selective advantage of the brown phase in bears, it need only be slight. It seems possible from my observations that climate is involved in maintaining the central Rocky Mountain brown population through a greater tolerance by sub-adults of the brown phase to arid conditions during spring and early summer. It would be interesting to experiment with the relative tolerance of light and heat by these two colour phases in the bear.

APPENDIX 3

HORMONAL ACTIVITY OF CERTAIN BEAR FOODS

Many plants fed to domestic livestock contain estrogenic substances (Kitts, 1960; Bickoff, 1961) and anti-estrogenic substances (Adler, 1962; Cook and Kitts, 1964), and both compounds at certain times of the year have deleterious effects on the reproduction of laboratory animals. The compounds are readily taken in through the digestive system, and their presence can be easily detected with bioassays. Since bears on Big Creek are almost exclusively vegetarians (Tisch, 1961) and concentrate on certain plant foods at each season of the year, I postulated that some of these foods might play a role in determining bear reproductive rates as has been shown to be the case in sheep by Bennetts *et al.* (1946). My hypothesis was that similar external hormones could be present in plants eaten by bears and that they might disrupt the critical endocrine balance necessary either for ovulation, implantation, or maintenance of pregnancy before implantation. Experimentally, ovulation can be prevented and pregnancy can be terminated with injections of synthetic hormones (see page 168). The period during which the unimplanted blastocysts are carried loose in the uterus has been suggested as a critical period for the pine marten by Enders and Pearson (1943). The assumption was made in this study that this might also be a vulnerable period for bears, and bioassays were made of foods abundant in the diets of bears during the breeding season, during the delay period, and near implantation time.

Several bear foods were collected, and bioassays were made to determine their estrogenic and anti-estrogenic activity. The samples were collected on the study area at the time the plants were being eaten and they were then frozen until the bioassays could be made. The bioassays of forage plants were undertaken on female rats using the technique described by Biely and Kitts (1964). Ostrovasky and Kitts (1963) have shown that similar substances are readily absorbed through the digestive system of rats and the assumption was made that they would be similarly absorbed in bears.

Four bear foods that are eaten in large quantities during periods that could be critical were tested. Chloroform (anti-estrogenic) and ether (estrogenic) extracts from huckleberries were highly toxic when injected into experimental rats (Table 20). In the 1965 experiments all rats died within a few minutes after the huckleberry injections, but in the 1966 experiments enough of the rats lived to show that the berries had no hormone-like activity. Even though attempts had been made to purify the extracts, they caused massive hemorrhages and inflammation of the viscera.

Plant Species	Treatment Groups (N = 6)											
	Control (saline)			Estradiol-17-β			Fraction A (estrogenic)			Fraction B + estradiol-17-β (anti-estrogenic)		
	B.W.	U.W.	M.U.W. as Per Cent B.W.	B.W.	U.W.	M.U.W. as Per Cent B.W.	B.W.	U.W.	M.U.W. as Per Cent B.W.	B.W.	U.W.	M.U.W. as Per Cent B.W.
Pinus albicaulis												
Whole seeds ± S.D.	46.6*	21.5 ±0.005	0.046	49.7	33.9 ±0.008	0.071	51.3	24.4 ±0.010	0.048	47.5	36.8 ±0.017	0.078
Meat only ± S.D.	"	"	"	"	"	"	49.9	40.4 ±0.016	0.081	48.8	38.3 ±0.020	0.078
Shell only ± S.D.	"	"	"	"	"	"	53.4	36.8 ±0.002	0.069	52.0	27.6 ±0.012	0.054
Heracleum lanatum ± S.D.	50.9*	66.7 ±0.010	0.131	55.0	80.8 ±0.023	0.148	51.5	69.3 ±0.041	0.135	40.9*	32.0 ±0.018	0.076
Angelica dawsoni ± S.D.	"	"	"	"	"	"	48.3	52.1 ±0.018	0.108	49.3	56.7 ±0.028	0.114
Vaccinium membranaceum ± ± S.D.	"	"	"	"	"	"	53.8**	48.9 ±0.015	0.092	52.3	77.2 ±0.013	0.148

**N = 4 *N = 5

Table 20. The effect of subcutaneous injections of ether (Fraction A) and chloroform (Fraction B) extracts on the uterine weight of laboratory rats (B.W. = mean body weight in grams when sacrificed, U.W. = mean uterine weight in mg., M.U.W. = mean uterine weight expressed as a percentage of body weight ± standard deviation). The meat of *Pinus* seeds was highly estrogenic; *Heracleum* was strongly anti-estrogenic.

Two of the plants tested gave significant results and need further comment: (1) the seeds (meat only) of the whitebark pine were found to be highly estrogenic, and (2) the entire plant of cow parsnip was found to be extremely anti-estrogenic. Neither of these species is distributed generally over the study area (Figure 31); therefore only a portion of the bear population would have access to large quantities of each food. Bears feed on the cow parsnip extensively in the late spring and early summer and on whitebark pine cones for a short time in early September (Tisch, 1961). White clover, a favoured food of certain Big Creek bears during late spring, has also been shown by Biely and Kitts (1964) to be anti-estrogenic.

The consumption of anti-estrogenic compounds by domestic stock has been shown sometimes to disrupt or prevent the onset of estrus by inhibiting maturation of follicles (Bennetts _et al_., 1946). This study has shown that before and during the breeding season some bears on Big Creek eat white clover and great quantities of cow parsnip, both of which contain powerful anti-estrogenic compounds. The potential for upsetting reproduction is obvious, providing my assumption is valid that these substances, too, are readily absorbed from the digestive tract. Cow parsnip is circumpolar in distribution, and it has probably been an important bear food throughout the evolution of black bears. It could be argued, therefore, that bears would have acquired tolerance to these substances. The matter requires further experimental

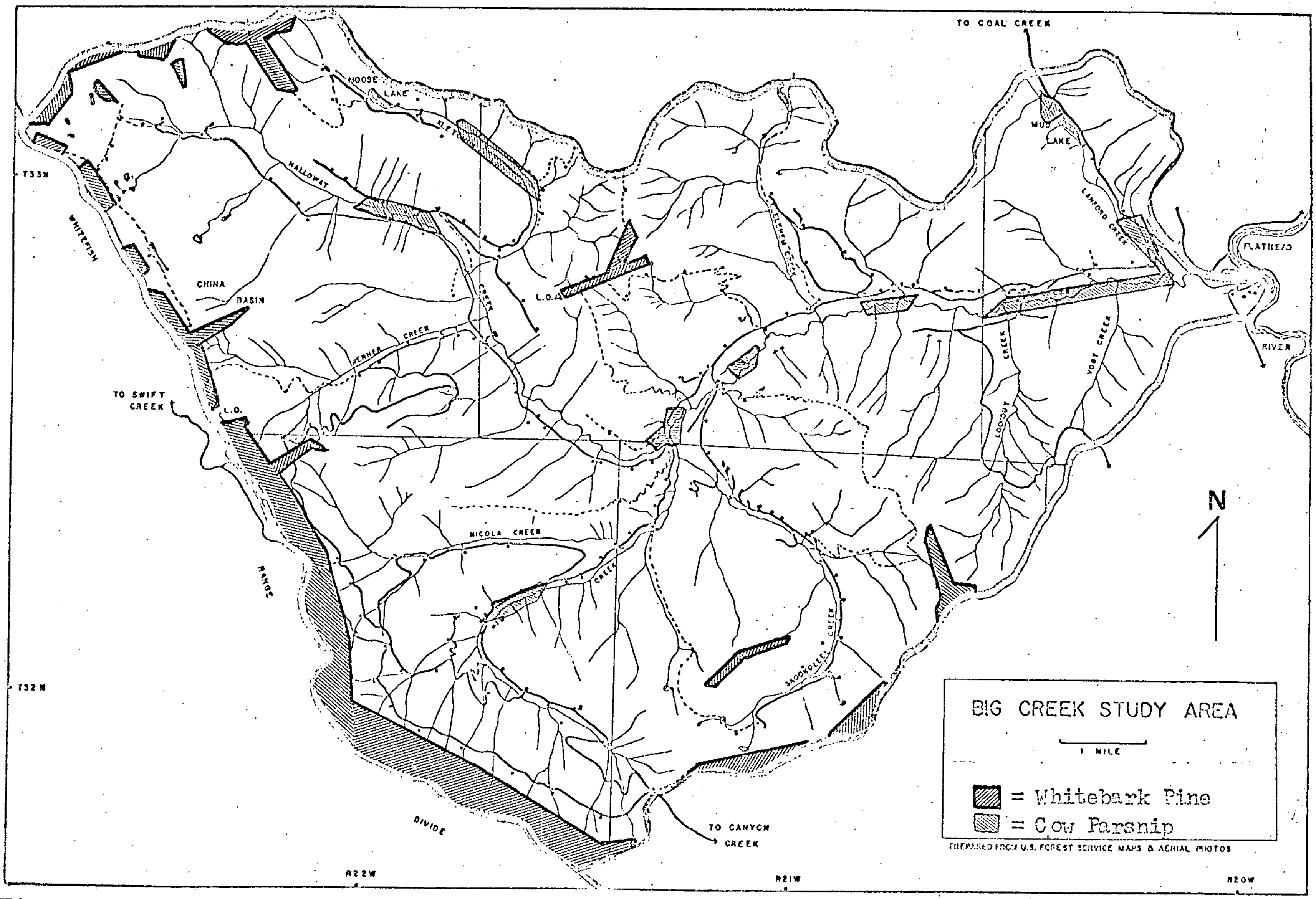

Figure 31. The approximate distribution of whitebark pine and cow parsnip on the Big Creek study area.

study, however, as there is some indication that cow parsnip does disrupt the estrous cycle. For example, one female (No. 61) resident in an area on Langford Creek where cow parsnip is abundant had not yet produced cubs in 1965 when she was 5-1/2 years old. She was in estrus later than normal in the breeding season of 1965, but unfortunately I was not able to locate her in the spring of 1966 to determine whether she had young. Cow parsnip sometimes forms almost the total diet for days or weeks at times when a bear's reproductive cycle could be vulnerable to interference. In a related study Pinter and Negus (1965) fed dry or sprouted wheat to different groups of _Microtus montanus_, and with their data they proposed that compounds present in the green shoots were responsible for better reproductive performance by controlling the timing of estrus. Bears living in an area abundant in cow parsnip should be compared with bears in neighboring areas eating other foods.

Estrogen-like substances which may contribute to extensive reproductive failure by causing the loss of young are also present in bear foods. Data obtained by Wimsatt (1963) indicate that during the delay period the black bear blastocyst must be in a progestational uterus. Both Wimsatt (1961) and Erickson and Nellor (1964) thought that corpora lutea in bears stayed functional until parturition. An increased growth of ovarian follicles in the fall before implantation, also reported by Wimsatt (1963), suggests that there is additional estrogen production then. Perhaps this increase in estrogen triggers implantation of the blastocysts in bears just as it does in the rat and mouse (Nutting and Meyer, 1963; Mayer, 1963; Shelesnyak and Kraicer, 1963; and others). An earlier or later surge of estrogen-like substances into the system from plant sources could easily disrupt the balance necessary for implantation or survival of blastocysts. Experimentally, estrogen has been shown to interfere with implantation in rats when given in large doses (Nutting and Meyer, 1963). Parkes and Bellerby (1926) using mice and Greenwald (1957) using rabbits have shown that a postimplantation increase in natural estrogens will result in embryo loss. Brambell _et al_. (1948) working with rabbits and Balser (1964) using wild coyotes (_Canis latrans_) showed similar effects using the synthetic estrogenic compound stilbestrol.

Whitebark pine nuts are eaten by bears in large quantities for a short period in the fall when they contain strongly estrogenic compounds. Also whitebark pine trees grow only in narrow strips of the total bear range in western North America, and the nuts are abundant only on certain falls. This periodic abundance of cones and the restricted distribution of the trees would prevent any genetic selection in the bear population to avoid hormonal upsets of reproduction. There was no heavy cone crop during the study, and therefore comparative data could not be gathered on the study area.

The possibility of anti-estrogenic substances in cow parsnip upsetting the estrous cycle in bears or of estrogenic substances in whitebark pine nuts terminating pregnancy by upsetting the uterine environment is highly speculative. It should be pointed out in a study of this nature, however, in order to emphasize that these factors may be important in wild populations. Animal physiologists and agricultural scientists have done much recent work in this field, but scientists working with natural populations have largely ignored this potential interference with normal reproduction. This neglect apparently follows from the assumption that since food supply does not change greatly during population changes (Rausch, 1950; Chitty, 1960; and Krebs, 1964), the change in food quality probably is not great.