THE ECOLOGY OF WINTER DEN SITES OF GRIZZLY BEARS IN BANFF NATIONAL PARK, ALBERTA

G. WILLIAM VROOM, Warden Service, Banff National Park, Alberta
STEPHEN HERRERO, Faculty of Environmental Design and Department of Biology, University of Calgary, Calgary, Alberta
R. T. OGILVIE, Curator of Botany, Provincial Museum, Victoria, British Columbia

Abstract: Forty-seven completed and partially dug grizzly bear (*Ursus arctos*) dens were examined in Banff National Park, Alberta, Canada, in 1975-76. The following environmental parameters were measured or estimated at most den sites: slope, aspect, altitude, soils, vegetation, snow accumulation, and age. Most environmental parameters studied had low variability. They appeared to be important in relation to dens that were physically stable for at least 1 winter, and where snow accumulation and perhaps thermal inversion contributed to energy conservation within the den. When environmental parameters associated with dens in Banff Park are compared with those found for grizzly/brown bear dens elsewhere, some parameters, such as slope angle and snow accumulation, are similar; others, such as elevation and aspect, are dissimilar. Despite the differences, which appear to be due to local biogeoclimatic factors, a comparison of data from various areas yields a consistent, general picture of the ecology of grizzly bear den sites.

Characteristics of grizzly bear winter dens were first described in the scientific literature by Murie (1944, 1961) and Clarke (1944). In Banff National Park, our study area, McCowan (1936) reported that grizzlies denned at high elelvations, but he gave no further details. Today a fairly extensive literature describes aspects of grizzly/brown bear winter den ecology in different biogeoclimatic zones (Ustinov 1960, Sokov 1969, Craighead and Craighead 1972, Lentfer et al. 1972, Zunino and Herrero 1972, Pearson 1975, Harding 1976).

In northern latitudes, winter dens are normally dug into the earth and certain environmental parameters related to the den sites appear to be reasonably consistent from area to area. Examples of these parameters are: slope angle where the den is dug, snow-holding ability of the site, and drainage of the soil. Exceptions are the 10 undug dens that were found in rock caves located on the north slope of the Brooks Range (Quimby 1974). Other environmental parameters associated with dug dens, such as compass orientation and altitude, vary from one area to another. In a broad perspective, grizzly/brown bears in northern latitudes appear to prefer dens that will remain physically stable for the duration of at least 1 winter and where snow and accumulation contributes to energy conservation by the bear during hibernation.

Because den site selection by grizzly bears depends partly on local conditions, certain environmental parameters of the den sites are different in each biogeoclimatic zone. For this reason, persons responsible for managing grizzly bears in a given biogeoclimatic zone require specific information on den site ecology. The present study, which was undertaken within the boundaries of Banff National Park, was intended to identify specific den locations and conditions and to describe environmental parameters that could be used to predict possible future denning areas. Winter den sites should have similar environmental parameters in other portions of the eastern slopes of the Rocky Mountains in Alberta. Exceptions might occur in far northern and southern portions of the range or in areas where prevailing wind direction is different during winter months.

The study was assisted by many people. D. Hamer, D. Holroyd, and P. Perren each contributed very substantially. F. Jaggi helped us find 1 major denning area. Several other members of the Banff Park Warden Service assisted in locating dens. The project would not have been possible without the services of J. Davies of Bow Helicopters, who not only flew for us but also found dens in his spare time. The study was financially supported by Parks Canada and the National Research Council of Canada.

STUDY AREA

The physiography of Banff National Park is one of extreme relief. The lowest valley bottoms lie at 1,300 m above sea level, and the higher summits extend up to 3,000-3,500 m. The mountain system consists of a complex series of parallel-aligned ranges: the eastern mountains comprising the Front Ranges are separated by a major thrust fault from the mountains of the western Main Ranges. Important climatic and vegetative differences are associated with these different mountain ranges.

The climate is continental, and over much of the park the air masses are dry, humidity is low, and precipitation and snowfall are low, especially toward the Front Ranges. Annual and winter temperatures are low, and there is a wide range in daily maximum and minimum temperatures and in seasonal temperatures. The continentality of the climate decreases westward into the Main Ranges and with increasing elevation. Here there is greater total precipitation and deeper snowfall. The maximum precipitation occurs in winter.

Several biogeoclimatic zones occur in Banff National Park (Ogilvie 1976): the Douglas-Fir Forest Zone (1,200-1,500 m) on the warm, dry, southerly-facing slopes; the Subalpine Forest Zone (1,300-2,300 m) which forms an extensive forest band from valley bottom to timberline; and the Alpine Zone (2,200-3,000 m) above timberline.

Banff National Park covers 6,564 km^2; approximately a third of this area (2,188 km^2) was surveyed from a helicopter in our search for dens. Intensive exploration for dens took place both from helicopter and on foot throughout a 128 km^2 portion of the study area. Winter den sites of grizzly bears were found within the Upper Subzone of the Subalpine Biogeoclimatic Zone at 2,000-2,300 m. Here, the total precipitation and snowfall are high, and the growing season is brief. The continuous forest becomes diffused with glade openings and is fragmented into islands at higher elevations. Ultimately it becomes small scattered colonies of dwarf krummholz. The tree species forming the forest are subalpine fir (*Abies lasiocarpa*), subalpine larch (*Larix lyallii*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*). The most widespread plant associations of this subzone are the grouseberry (*Vaccinium scoparium*)-heather (*Phyllodoce* spp.-*Cassiope tetragona*) association and the false azalea (*Menziesia ferruginea*)-rhododendron (*Rhododendron albiflorum*) association. Avalanche tracks cutting into this forest are dominated by the tall herb-grass meadow (*Elymus* spp.-*Bromus* spp.) association on southwesterly slopes and the willow (*Salix* spp.) association on northeasterly slopes.

METHODS

In April 1975, we began helicopter flights to acquire information on winter den sites and early spring movements of grizzly bears. We found the first den on 9 May 1975. Discovery of this den gave us a preliminary idea of the environmental parameters related to choice of den sites. From then on, we employed a combination of aerial searches supplemented by ground searches to discover dens.

Dens were visible from the helicopter when snow was on the ground in spring (3 dens) and also during nonsnow seasons (8 dens). A pile of tailings material accumulated during den excavation extended 3-7 m below what we assumed were completed dens. Whenever the vegetation was sufficiently open and there was no snow on the ground, these tailings piles were easily seen from a helicopter.

Once a den site was discovered by aerial search, it and the surrounding area were thoroughly explored on foot. Normally, a helicopter was used for morning placement of personnel near a suspected den sit.

One group of dens was found in response to observations made by a Banff townsite resident. Another den was found during a study of grizzly bear food habits and habitat preferences.

Our methods for discovering dens were subject to certain biases. Although we were unlikely to find dens that were well hidden in trees, many dens were discovered in forested areas. These discoveries, however, usually occurred after a den was located in a nearby open or semi-open area. We also searched forested areas that we thought had appropriate environmental conditions for dens but where no dens had been seen from the air. The biases could be checked through the use of biotelemetry, but at the time of the study the park had a policy of not employing this technique.

Another bias of the study was the different intensity of search effort accorded to various areas of the park. Some portions, especially the Cascade Valley, were searched intensively, other areas less intensively, and some possible denning habitat has not yet been searched.

Each den site was eventually examined on the ground. While there, we numbered and photographed the den site and recorded environmental parameters. A clinometer was used to record slope angle and a steel tape was used to take standardized measurements of the den. Altitude was estimated with a pocket altimeter that had been set that morning in Banff. Exposure was recorded by taking a compass bearing. Estimates were made of the relative abundance of different species within tree, shrub, herbaceous, and ground layers near the den. In one instance, measured plot analysis was carried out.

The soil profile was examined from a newly exposed section at the den opening for horizon, depth, color, texture, structure, and consistency. The soil morphology and classification were based on criteria of the Canadian Soils Classification System (Canada Department of Agriculture 1974).

RESULTS

Results reported in this paper are for the period 20 April 1975-20 November 1976. During this time we recorded data for 47 den sites. Twenty-nine of these were judged to be completed dens, previously used by grizzly bears during winter. The remainder were partially dug dens, most likely made by grizzly bears but probably not used during winter. These partially dug dens averaged 1.1 m in overall length. They usually did not have a chamber.

We assumed that a den had been used during a winter if it appeared similar in size to the dens where we actually saw grizzly bears inside (1 den) or saw fresh tracks just outside the den (2 dens). We consider it unlikely that the excavations that we assumed were made by grizzly bears where in fact made by black bears (*Ursus americanus*) or other animals. A few black bear dens have been found in Banff National Park (Herrero 1970, wardens' wildlife observation cards), but all were at lower elevations. In addition, black bears are very rare or absent in the upper portions of the Cascade Valley, where 13 completed dens and 3 partially dug dens were found. The paucity of black bears in this region was confirmed during intensive field work during 1974-76. This work included the use of ungulate carcasses to attract bears. No black bears were observed to visit these carcasses.

We considered the possibility that the holes that we called winter dens might in fact be day beds for warm-season use. Despite possible confusion in this regard (Craighead 1972, Craighead and Craighead 1972), we consider a misjudgment unlikely. During the past 3 years of field work on grizzly bears in Banff Park, numerous day beds were found. These beds were always shallow excavations very unlike winter dens. Also, most sites where we found dens were not foraging areas, except perhaps casually near the den site.

Ages of Dens

The dens that we found were estimated to be of various ages (Table 1). The age of most of those dens

Fig. 1. Grizzly bear den in avalanche meadow vegetation type, Banff National Park, spring 1976. Photo of same den, taken from a helicopter, is shown in Fig. 8.

where grizzly bear or fresh tracks were not seen was estimated by noting the vegetation regrowth on the tailings pile or den mouth (Fig. 1) and the extent of collapse

Table 1. Estimated ages of grizzly bear dens, Banff National Park, 1975-76.

Estimated age (years)	1-2	3-4	6-9	10-15	15-20	20-25	>25
Number of dens	10	7	3	6	1	1	3

of the den. According to estimates by our plant ecologist, after a maximum of 75-100 years, vegetative or geomorphological traces of collapsed grizzly bear dens are no longer readily discernible. Age estimates were not made for some dens.

Spatial Distribution of Dens

Several dens were usually found near one another. These dens were separated by as little as 40 m or as much as several kilometers. Dens probably tended to be clustered because only a small portion of the total area of Banff Park seemed to provide suitable conditions for grizzly bear dens. Table 2 shows the number of com-

Table 2. Number of completed and partially dug grizzly bear dens in each topographically distinct area, Banff National Park,1975-76.

Area	A	B	C	D	E	F	G	H	I	J	K
Number of dens	2	14	2	2	2	7	6	5	2	1	4

pleted and partially dug dens found in 11 topographically distinct areas.

To avoid disturbing grizzly bears in denning areas, specific locations are not given; they are on file with the Banff Park Warden Service.

Time of Denning and Emergence

Warden wildlife observation cards and reports from other reliable observers suggest that in Banff National Park, most grizzlies normally den sometime during November and emerge about early April. Detailed field observations were carried out in the Cascade Valley from October 1975 through November 1976. During fall 1975, the last grizzly bear tracks, those of a female and 2 cubs-of-the-year, were seen on 13 November. The first grizzly bear tracks appeared on 20 March 1976. The last tracks in 1976 were made about 15 November. In Jasper National Park, which is in a similar biogeoclimatic zone, the use of radiotelemetry revealed the latest denning date to be 16 December (Russell, personal communication). We assume that, on the average, grizzly bears in Banff National Park spend 4.5 months in or near their den sites. Variations in this time span have been reported elsewhere and are related to age- and sex-classes of grizzly bears (Craighead and Craighead 1972, Lentfer et al. 1972, Pearson 1975) as well as to climate.

Physical Configuration of Dens

Dens were dug approximately horizontally into slopes. They appeared to contain (or have contained) a tunnel and a chamber, the chamber being larger in height and width than the tunnel. The average dimensions for the 29 dens that we judged to have been used were: width of entrance, 0.72 m; height of entrance, 0.68 m; total length from entrance to back of den, 2.20 m; maximum width of chamber, 1.22 m; maximum height of chamber, 0.84 m.

Partially Excavated Dens

The partially dug dens that we found were all located near completed dens. They appeared to be excavations that grizzlies had begun but had abandoned when unsuitable microenvironmental conditions were encountered. Often a large rock blocked further excavation. In altitude, aspect, and slope angle, partially dug dens did not appear to differ from completed ones. Because of the environmental similarity between partially dug and completed dens, data on both are presented together.

ENVIRONMENTAL PARAMETERS OF DEN SITES

Altitude, Aspect, and Thermal Inversion

Both types of dens were found within a rather narrow altitudinal band (Fig. 2). The distribution approximated a statistically normal one, except for skewing on the low elevation end. The sharper cut-off at higher elevations was probably due to such environmental factors as increased stoniness of ground, shallow soils, and exposure to wind near ridgetops. Both types of dens were usually located quite high up in the valley sides but were beneath the ridge crests (Fig. 3).

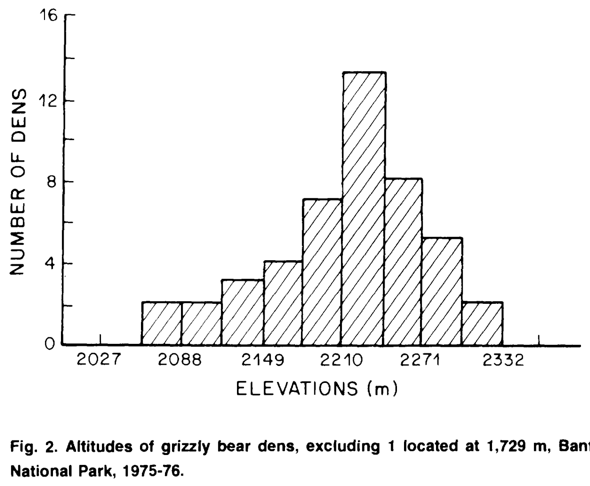

Fig. 2. Altitudes of grizzly bear dens, excluding 1 located at 1,729 m, Banff National Park, 1975-76.

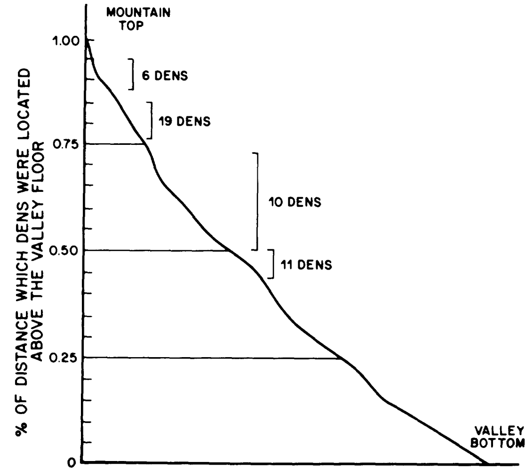

Fig. 3. Histogram and drawing depicting locations of grizzly bear dens expressed as a percentage of the elevation from valley floor to mountain top, Banff National Park, 1975-76.

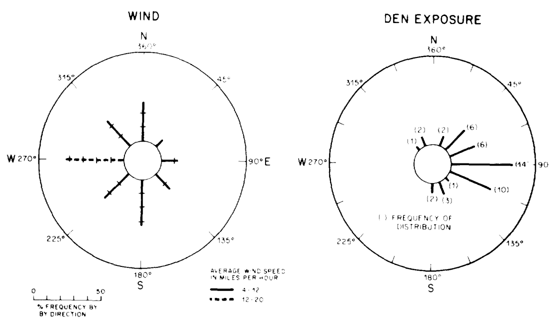

Fig. 4. Aspect of grizzly bear dens (Banff National Park, 1976) and wind force vectors (Calgary, Alberta, January 1961).

The aspects of 36 of 47 den sites were between 45° (NE) and 112.5° (ESE) (Fig. 4). The wind force vectors for Calgary, the nearest area for which such data are synthesized, are also shown in Fig. 4. The strongest wind force vector comes from the west and the most frequent den site aspect was eastward, exactly to leeward of the west wind. Den sites were located on leeward slopes, within zones of inferred snow deposition.

Thermal inversion is another environmental variable that may be related to the altitude of den locations. In the Rocky Mountains, inversions are prevalent east of the western Main Ranges and occur in most valley systems within the study area. When thermal inversions occur, a layer of warm air functionally traps a lower layer of cold air beneath it, resulting in cooler temperatures at lower elevations. Grizzly bears dens were located at alititudes where preliminary data suggests that thermal inversion is a prevalent phenomenon.

Slope Angle

Fig. 5 shows that grizzly bear dens were quite specific with regard to slope angle of the den locations. The mean slope angle for completed and partially dug dens considered together was 33°. All dens were on slopes greater than 22°, with 36 of 46 dens between 30° and 38°; none were on slopes over 40°.

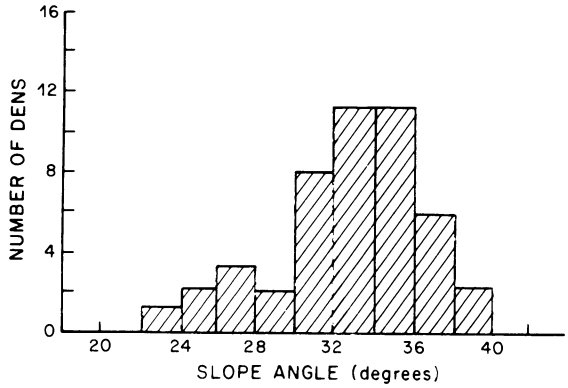

Fig. 5. Angle of slope where grizzly bear dens were located, Banff National Park, 1975-76.

Soils and Vegetation

The soil profiles of the dens consist of Podzolic, Brunisolic, Chernozemic, and Regosolic soils. The soil parent materials include tills, colluvium, and fragmented or weathered bedrock. The rock types include limestones, shales, sandstones, conglomerates, and quartzites. The vegetation in which the dens are located consists of mature forest, krummholz, meadow, and shrub communities.

The soil and vegetation data are summarized for 38 dens under the following 6 vegetation types (Ogilvie 1966). Soils and vegetation data were not collected for the remaining 9 dens. The major plant species are listed, by strata, in order of dominance.

1. Grouseberry-Heather Vegetation Type. *Picea-Abies-Larix/Vaccinium scoparium* Association (Figs. 6, 7).

Seventeen completed and partially dug dens.

Shallow Podzolic Soils (LFH, Ae, Bf, C); parent material: scattered to very abundant colluvial fragments of shale, sandstone, or limestone. The vegetation is characteristic of the upper subalpine and timberline area,

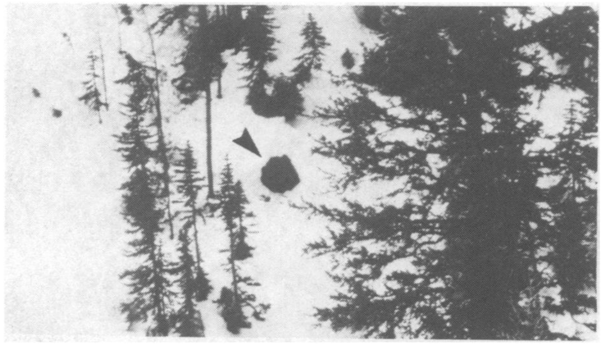

Fig. 6. Aerial photograph of grizzly bear den in grouseberry-heather vegetation type, Banff National Park, spring 1976.

Fig. 7. Close-up photograph of den shown in Fig. 6. Note supporting tree root.

consisting of mature closed stands, stands with openings, and low krummholz colonies. The tree composition is spruce, subalpine fir, and sometimes subalpine larch. The stand structure varies from small openings under the tree canopy to large glades. There is very deep snow accumulation that increases with increasing size of the glade.

Trees: *Picea engelmannii, Abies lasiocarpa, Larix lyallii.*

Shrubs: *Vaccinium scoparium, Phyllodoce glanduliflora, P. empetriformis, Cassiope tetragona, Vaccinium myrtillus.*

Herbs: *Arnica latifolia, A. cordifolia, Pedicularis bracteosa, Erigeron peregrinus* var. *callianthemus, Valeriana sitchensis, Potentilla diversifolia, Hieracium gracile, Silene lyallii, Castilleja rhexifolia, Antennaria racemosa, A. lanta, A. alpina.*

Mosses and lichens: *Dicranum scoparium, D. fuscescens, Timmia austriaca, Peltigera aphthosa, Cladonia* spp.

There are 4 important variants of this habitat type:

a. Shallow bedrock variant: the bedrock occurs close to the surface and the shallow soil mantle consists of coarse quartzite rock fragments; the soil profile is Regosolic (LFH, (B), C).

b. Moist seepage variant: the soil profile is a Seepage Regosol (LFH, B, C); the parent material is compact clay loam with coarse shale fragments. The seepage indicator species are: *Salix vestita, Parnassia fimbriata, Equisetum scirpoides, Anemone parviflora, Senecio lugens.*

c. Dense krummholz variant: the vegetation consists of a dense colony of *Abies*, with very sparse occurrence of other species: *Arnica cordifolia, Valeriana sitchensis*. The soil profile is a leached Brunisol (LFH, Bf, C); the parent material is abundant, hard shale fragments.

d. Large glade with deep snow accumulation: the deep snow indicator species are: *Salix arctica, Myosotis alpestris, Stellaria monantha*. The soil profile is Shallow Chernozemic Black (LFH, Ah, B, C); the parent material is sandy loam with scattered stones.

2. False Azalea-Rhododendron Vegetation Type. *Picea-Abies-Larix/Menziesia-Rhododendron* Association.

Five completed dens.

Deep Podzolic Soils (LFH, Ae, Bf, C); the soil parent material is variable: tills of stones and loam, weathered shales of very fine particles or with stone fragments. This vegetation type occurs at slightly lower elevations than the previous one; it consists of old, mature, closed stands of spruce, fir, and occasionally larch.

Trees: *Picea engelmannii, Abies lasiocarpa, Larix lyallii.*

Shrubs: *Menziesia ferruginea, Rhododendron albiflorum, Vaccinium membranaceum, V. myrtillus, V. scoparium.*

Herbs: *Arnica cordifolia, A. latifolia, Viola orbiculata, Cornus canadensis, Lycopodium annotinum, Pedicularis bracteosa.*

Mosses and lichens: *Hylocomium splendens, Peltigera aphthosa, Dicranum fuscescens.*

3. Fir Krummholz-Rock Willow-Herb Vegetation Type. Krummholz *Abies/Salix vestita-Thalictrum* Association.

Five completed dens.

Deep Podzolic Soils (LFH, Ae, Bf, C); the parent material is coarse colluvial limestone rubble.

There is deep snow, with surface avalanching down to the top of the krummholz vegetation. This vegetation type occurs at timberline and consists of dense fir krummholz.

Trees: *Abies lasiocarpa* (krummholz form).

Shrubs: *Salix vestita.*

Herbs: *Thalictrum occidentale, Senecio lugens, Valeriana sitchensis, Arnica cordifolia, Epilobium angustifolium, Fragaria virginiana* var. *glauca.*

Mosses and lichens: *Brachythecium* sp., *Peltigera aphthosa.*

4. Subalpine Herb-Meadow Vegetation Type.

Two completed/dens.

Shallow Podzolic Soil (LFH, Ae, B, C); parent material: loam with scattered stones.

The structure of the vegetation is an herb-meadow glade-opening in the upper subalpine forest.

Trees: *Abies lasiocarpa, Picea engelmannii, Larix lyallii.*

Herbs: *Hedysarum sulphurescens, Epilobium angustifolium, Heracleum lanatum, Fragaria virginiana* var. *glauca, Achillea millefolium, Valeriana sitchensis, Thalictrum occidentale, Erythronium grandiflorum.*

5. Avalanche Meadow Vegetation Type. *Elymus innovatus-Bromus pumpellianus-Hedysarum sulphurescens* Association (Figs. 1, 8).

Seven completed dens.

Fig. 8. Aerial photograph of grizzly bear den in avalanche meadow vegetation type, Banff National Park, spring 1976. A female and 3 cubs-of-the-year were inside.

Shallow Chernozemic Black Soil (Ah, B, C) and Shallow Brunisolic Soil (LFH, (Ah), Bf, C); parent material: loam and shale fragments. This vegetation consists of rich meadows of mixed grasses and forbs occupying avalanche tracks cut into the upper subalpine closed forest.

Shrubs (infrequent): *Juniperus communis.*

Herbs: *Elymus innovatus, Bromus pumpellianus, Hedysarum sulphurescens, Aster foliaceus, Fragaria virginiana* var. *glauca, Danthonia spicata, Epilobium angustifolium, Poa* spp., *Festuca scabrella.*

Mosses and lichens (infrequent): *Tortula ruralis, Bryum* sp., *Brachythecium* sp., *Peltigera canina.*

There are 2 variants of this vegetation type:

a. With additional grass species: *Agropyron trachycaulum, Trisetum spicatum, Phleum alpinum, Danthonia spicata, Aster foliaceus.*

b. With heavier shrub cover: *Juniperus communis, Arnica cordifolia, Elymus innovatus.*

6. Subalpine Shrub-Herb Meadow Vegetation Type Two dens.

Shallow Chernozemic-Regosolic Soils (LFH, (Ah), B, C); parent material: colluvial limestone fragments.

The vegetation occurs in the upper subalpine krummholz and consists of mixed shrubs and meadow herbs.

Trees (krummholz form): *Abies lasiocarpa, Picea engelmannii.*

Shrubs: *Juniperus communis, Potentilla fruticosa, Salix glauca.*

Herbs: *Aster* spp., *Solidago multiradiata, Epilobium angustifolium, Fragaria virginiana* var. *glauca, Achillea millefolium, Agropyron latiglume, Bromus pumpellianus.*

Summary of Typical Den Site Conditions

A "typical" den was located in the upper subalpine-timberline area at a mean elevation of 2,280 m. The mean slope angle was 33°, and the orientation was between 22.5° (NNE) and 112.5° (ESE). Slopes of typical dens are leeward of prevailing winds and partly because of their lee position have stable, deep snow cover. Surface avalanching may occur but does not normally extend to the ground surface.

Soils are well-drained; wet-seepage soils are avoided. The typical den may be located in diverse geological bedrocks and parent materials. Shallow bedrock soils are avoided. The soils have a wide range of stoniness and amounts of sand, silt, and clay. Extremes of soil textures are avoided, e.g., massive rock blocks or very fine clays. The structural coherence of the soil mass is variable, ranging from weak to strong. Weakly coherent soils may be structurally reinforced by a network of roots of trees, shrubs, and herbs and by being frozen during winter usage of the den.

Aberrant Dens

Some dens varied so much from the norm that special mention is required.

One den was much lower in elevation (1,769 m) than the others. The roof of this den was formed by a substantial root of a spruce tree. Then den was large enough to have been used and could have been either a black bear or grizzly bear den.

Five dens were oriented either southerly or northwesterly, possibly exposing them to strong wind or winter sun. We have an impression that local microclimatic factors (such as nearby ridges) lessened the potential adverse effects of wind. However, some of these dens did not seem to be as climatically buffered as were most dens.

Two dens located about 40 m apart appeared to have collapsed during their first winter. When we found them they appeared to be less than a year old. One was probably unused and the other used for a month or two before it collapsed. Near these sites, 38 trees had broken limbs or boles. Limbs were removed to a height of 4.6 m, apparently indicating that the bear had climbed the trees since maximum snow depths would not have exceeded 2 m. A substantial ground bed, at least 30 cm thick when we examined it during late summer, was located in front of 1 den. We surmised that the bear had spent the remainder of the winter or spring on this bed.

Observations of Grizzly Bears at a Den Site

On a helicopter search flight on 12 April 1976, we saw a female grizzly and 1 cub-of-the-year at an open den entrance. At this time there were no tracks in the snow outside of the den. On 17 April, the den was checked again and there were still no tracks. On 21 April, a single track appeared outside the den. From 23 April to 25 April, one of us used the helicopter to set up a bivouac camp about a kilometer from the den. The bears and the den site were observed from this camp with the aid of a spotting scope (20X, 20-45X). The den occupants were a female grizzly bear with 3 cubs-of-the-year. During the time the den site was observed, the bears were outside for 2-4 hours per day, spending each night (23 and 24 April) inside the den. While the female was outside, her behavior and that of the cubs differed markedly. The cubs either played or nursed, or occasionally rested, when outside. Their play was vigorous and prolonged but never took them farther than 20 m from the female. One of their play activities was to climb up a snow slope and then launch themselves down it. They sometimes started their slide from about 4 m above the den mouth. At these times their slide normally stopped when they landed on the head of the female who sat in the den entrance. Her movements in general, even on those occasions, were lethargic. She allowed the cubs to fall off or climb down her back without taking action herself. When walking she would sometimes take slow, exaggerated steps, somewhat slothlike but faster. She occasionally ate snow, and subsequent examination of the site suggested that she dug some *Hedysarum sul-*

phurescens roots. She appeared still to be in her winter lethargy, conserving energy. The cubs were actively exploring their local environment.

The female built 2 day beds in patches of trees, 12 m and 15 m away from the den entrance. Trails worn in the snow connected these sites with the den. Other worn trails led to another patch of trees and to nearby assumed feeding areas where the snow had sloughed. The entire zone of activity was no greater than 50 m in diameter.

On 30 April, the den was checked again and the bears were gone. Snow coverage of tracks suggested that the bears may have left 2 or 3 days earlier. Therefore the family appeared to have spent about a week sleeping at night in the den and sometimes going outside during the day. Lentfer et al. (1972) found evidence that 3 family groups of grizzly bears in coastal Alaska had beds outside their dens. Their data indirectly suggest similar usage to that described here. Craighead and Craighead (1972) reported another similar observation for a female and 2 yearlings that remained near a den site for about 3 weeks after emerging.

DISCUSSION

This project was designed to conform to a Banff National Park policy directive that requested all possible information on winter den sites of grizzly bears but did not allow direct disturbance of the bears in any way. Because biotelemetry was not used, most of our work was necessarily inferential. We may have oversampled dens which were visible from the helicopter, and undersampled dens obscured by trees or thick shrubbery. We focused on the study of environmental parameters associated with den sites.

As was found in coastal Alaska (Lentfer et al. 1972), in the interior Yukon (Pearson 1975), and on the Arctic coast (Harding 1976), helicopter or fixed-wing aircraft is an efficient tool to help locate dens. In Banff National Park, it was profitably combined with searches on foot.

Most of the den sites that we investigated were older than a year. We found that most dens begin to disintegrate after the first winter and that after 75-100 years they are difficult to detect, even with experience. Reuse of dens in our area is unlikely because of collapse.

Environmental parameters associated with den sites were quite consistent in our study area. Dens of grizzly bears in Banff National Park appeared to be situated in areas when a deep insulating layer of snow would accumulate at the den entrance and above, and where the soils were cohesive enough during the first winter to maintain the physical stability of the den. The stored heat of the earth and the metabolic heat of the bear appear to have been conserved within the den.

The vegetative type widely used for winter dens is the grouseberry-heather association. Deep snow accumulates between widely spaced trees or in the glade openings in the stand. Another vegetative type frequently used for denning is the grass and forb meadows on avalanche tracks cut into the closed subalpine forest stands. Fewer dens were found in the krummholz shrub meadows and in the herb meadow glade openings. Some dens were found at lower elevations in the closed mature forest of the false azalea-rhododendron tall shrub vegetation type.

A common feature of all these vegetative types is the deep and long-lasting snow accumulation that we infer was associated with them. The specific action of avalanching in some of these communities is of importance here. The elevation of many dens and their locations on the leeward side of mountains often put them near the trigger zones of winter avalanches. Although the avalanche near the release point may pass directly over a den, it is unlikely that winter avalanches would often remove the snow cover to a depth that would seriously affect the insulation of the den. Winter avalanches of major size in the study area are normally released by a soft slab breaking in the trigger zone. This soft slab is usually only the upper layer of the snowpack. At these elevations, also, not many days would elapse after a surface avalanche released until a new layer of snow would be deposited, either by snowfall, wind action, or both, and any loss of insulation would be restored. After the avalanche has gained enough momentum going down the mountain, it will move the entire snowpack, but this would happen only at elevations lower than where grizzly dens are normally located.

The type of avalanche that does take the snow to the ground at elevations where dens are located is the wet spring avalanche. This type, however, is not likely to be a problem to the bears since it occurs in late spring, after the bears have left the dens.

Of the considerable diversity of soils and parent materials at the den sites, some common features should be mentioned. The soil profile types — Podzolic, Brunisolic, Chernozemic, and Regosolic — are all well drained; there are no Organic, Gleysolic, or Alluvial profiles. Soil texture, structure, stoniness, and consistency are highly variable, ranging from fine loams to coarse rock fragments and from loose coherence to very firm consistency. There are numerous combinations of these soil physical factors that can provide the requisite stability for dens during a single winter occupancy: a minimum amount of structural coherence of the rock fragments and fine soil particles, combined with the binding effect of a dense network of roots of trees, shrubs, and sod-grasses, along with the solidifying effect of the frozen soil mass.

There is no relationship between the dens and the bedrock geology. A wide range of rock types occur: limestones, shales, sandstones, conglomerates, and quartzites.

When the environmental parameters associated with den sites in Banff National Park are compared with those found elsewhere, a fairly consistent picture of denning ecology emerges. Environmental parameters are either consistent from area to area or much of the variability can be explained by considering local biogeographic conditions, the experience of a given bear, and perhaps human influence both today and over many generations.

Rock cave dens as found by Quimby (1974) are excluded from the following discussion.

The mean slope angle of den sites in Banff National Park was 33°, which compares closely with the findings of Lentfer et al. (1972) (9 dens, 0°-30°; 14 dens, 30°-45°; 5 dens, 45°-60°), Pearson (1974) (mean slope angle, 35°), and Harding (1976) (most dens, 30°-60°), Pearson (1974) (mean slope angle, 35°), and Harding (1976) (most dens, 30°-50°). We agree with Harding (1976) that slope angle seems to be important for trapping snow at the den entrance but not in the chamber and for easy removal of material dug during construction. A more important reason for choosing slopes of a certain angle may be related to the stability and thermal properties of the den. Grizzly bears normally dig straight into a slope. If they dug downward, the den would be a less efficient heat trap. If they dug straight into slopes of less than 25°, there would be a thinner covering of soil over the den and the chances of collapse would probably increase. Shallow, unstable soils, and the lesser ability of steeper slopes to hold snow are probably the factors that prevent grizzly bears from using very steep slopes.

Although the soils associated with Banff National Park dens were found under 6 different plant associations, all soil types were normally well drained and stable at least during the first winter. Amongst the exceptions were 2 dens that appeared to have collapsed during the first winter (see Aberrant Dens, RESULTS section). Perhaps these dens were made by inexperienced grizzly bears. Craighead and Craighead (1972) hypothesize that experience in den construction serves to improve what is for the most part genetically programmed behavior. Learning, both from the mother grizzly bear and from individual experience, would also be important within each biogeographic zone. Because specific environmental parameters vary from area to area, learning is a necessary adjustment.

Most authors have reported that willow and alder (*Alnus* spp.) shrubs are present at den sites (Lentfer et al. 1972, Pearson 1975, Harding 1976) or that dens are buttressed by tree roots (Craighead and Craighead 1972). Although some of our dens had buttressing tree or shrub roots (Fig. 7), most were in small glade openings in subalpine forest, in subalpine herb meadows, or in avalanche meadows. Buttressing tree or shrub roots were absent at many of these sites although typically there was adequate soil development and root penetration by herbs. Synthesizing from all reported studies, it appears that roots help bind the soil at dens, but in some areas like ours, trees or shrubs are not essential to support the dens, to hide them, or to catch snow.

The vegetation at den sites indicates that dens in Banff National Park are located in areas that accumulate snow. The aspect (predominantly NNE to ESE) of dens, form of vegetation, average mean altitude (2,280 m), and direction of prevailing winds (prediminantly W) are all favorable to early and prolonged snow accumulation at den sites. If the bears denned at lower elevations they would receive significantly less insulation from snow. Lower down, the snow comes later, is generally more dense, and is not as deep. In late fall, after heavy frosts, grizzlies appear to have difficulty finding adequate food. They move toward higher denning areas when ordinarily there is little snow in valley bottoms. Perhaps they go to the highest elevation where they still find good soil, aspect, and slope. It would seldom be long before snow would cover and thus insulate the den. The average altitude of den sites in Banff National Park also suggests the possibility that colder temperature normally associated with higher altitude may be ameliorated by thermal inversion effects.

LITERATURE CITED

Canadian Department of Agriculture. 1974. The system of soil classification for Canada. Can. Dept. Agric. Publ. 1455. 255pp.

CLARKE, C. H. D. 1944. Notes on the status and distribution of certain mammals and birds in the Mackenzie River and western Arctic area, 1942 and 1943. Can. Field-Nat. 58(3):97-103.

CRAIGHEAD, F. C., AND J. J. CRAIGHEAD. 1972. Grizzly bear prehibernation and denning activities as determined by radiotracking. Wildl. Monogr. 32. 35pp.

CRAIGHEAD, J. 1972. Discussion. Pages 134-135 *in* S. HER-

RERO, ed. Bears — their biology and management. IUCN Publ. New Ser. 23.

HARDING, L. 1976. Den-site characteristics of arctic coastal grizzly bears (*Ursus arctos* L.) on Richards Island, Northwest Territories, Canada. Can. J. Zool. 54(8):1357-1363.

HERRERO, S. 1970. A black bear and her cub. Animals 12(10):444-447.

LENTFER, J. W., R. J. HENSEL, L. H. MILLER, L. P. GLENN, AND V. D. BERNS. 1972. Remarks on denning habits of Alaska brown bears. Pages 125-132 *in* S. Herrero, ed. Bears — their biology and management. IUCN Publ. New Ser. 23.

MCCOWAN, D. 1936 (reprinted 1950). Animals of the Canadian Rockies. Dodd, Mead and Co., New York.

MURIE, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States. Natl. Park Serv. Fauna Ser. 5. 238pp.

———. 1961 (1963 cited edition). A naturalist in Alaska. The Devin-Adair Co., New York. 302pp.

OGILVIE, R. T. 1966. Ecology of vegetation in Banff National Park. National Parks Branch Workshop. 21pp.

———. 1976. Ecology of alpine and subalpine vegetation in the Rocky Mountains of Alberta. Proc. British Columbia Envir. and Land Use Secretariat. 25pp.

PEARSON, A. M. 1975. The northern interior grizzly bear *Ursus arctos* L. Can. Wildl. Serv. Rep. Ser. 34. 86pp.

QUIMBY, R. 1974. Grizzly bear. Pages 1-97 *in* R. D. Jakimchuk. ed. Mammal studies in northeastern Alaska with emphasis within the Canning River drainage. Canadian and Alaskan Arctic Gas Study Limited, Biol. Rep. Ser., Vol. 24.

SOKOV, A. I. 1969. The study of bears in Tadjikistan. Pages 185-189 *in* Problems of increasing productivity of hunting grounds. USSR Ministry of Agriculture, Moscow.

USTINOV, S. K. 1960. Annual life-cycle of the bear in the northeastern Baykal area. Proc. Irkutsk Agric. Inst. 18:207-210.

ZUNINO, F., AND S. HERRERO. 1972. The status of the brown bear (*Ursus arctos*) in Abruzzo National Park, Italy, 1971. Biol. Conserv. 4(4):263-272.