DENNING CHARACTERISTICS OF BROWN BEARS ON KODIAK ISLAND, ALASKA

LAWRENCE J. VAN DAELE, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518
VICTOR G. BARNES, JR., U.S. Fish and Wildlife Service, 1390 Buskin River Road, Kodiak, AK 99615
ROGER B. SMITH, Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615

Abstract: Investigations of brown bear (*Ursus arctos middendorffi*) denning ecology in 2 areas of Kodiak Island, Alaska, revealed that subpopulations of bears living within 70 km of each other had developed noticeably different denning behaviors. One hundred and fifteen radio-collared brown bears were located in 321 dens. The relative order in which bears in various reproductive categories entered their dens was similar in both study areas; females entered dens earlier than most males, and pregnant females generally entered dens earliest. Female bears in Southwest Kodiak generally entered their dens 2 to 3 weeks later than their counterparts in the Terror Lake area. We hypothesize that this variation was related to the relative food availability in the 2 areas during late autumn. Emergence chronology was similar in both areas. Males were generally the 1st group to emerge from their dens, and females with new cubs were usually last. Bears at Terror Lake preferred steep slopes in alpine habitat for den sites. In Southwest Kodiak, midslope habitat and moderate slopes were preferred denning habitat. Two areas with high concentrations of dens were identified in the Terror Lake area. A high degree of fidelity to specific den sites was exhibited by individual brown bears on Kodiak. Two notable anomalies in denning behavior were observed in this study; use of multiple dens by 27 bears and failure to enter dens by 8 bears. Management implications of the differences in the denning ecology of these subpopulations are discussed.

Int. Conf. Bear Res. and Manage. 8:257–267

The brown bear population on Kodiak Island is a valuable resource that is intensively managed. Recent investigations have verified that the island supports one of the densest populations of brown bears recorded, with an estimated mean density of 1 bear/4.1 km^2 (Barnes et al. 1988). Approximately 130 bears are harvested annually by sport hunters (Alaska Department of Fish and Game [ADF&G] files) and the island has a reputation for producing large trophies (Nesbitt and Wright 1981). In recent years there has also been an increase in the number of people visiting the island to view and photograph bears.

Past studies of bears on Kodiak have focused on feeding habits (Clark 1957, Clark 1959, Atwell et al. 1980), reproduction (Hensel et al. 1969), movements (Berns and Hensel 1972, Berns et al. 1980) and harvest (Troyer 1961, Troyer and Hensel 1969). Although only limited attention has been given to denning (Lentfer et al. 1972), information on denning ecology has utility for avoiding disturbance to bears in their dens and in regulating harvest (Schoen et al. 1987).

We investigated brown bear ecology in 2 separate areas of Kodiak Island from 1982 to 1988 (Barnes 1986, Smith and Van Daele 1988, Smith and Van Daele 1990). Brown bear subpopulations in the 2 areas lived within 70 km of each other, but occupied dissimilar habitats. Comparison of the denning ecology of these bears provided an interesting contrast in how they had adapted to exploit each habitat successfully .

Funding for the research at Terror Lake was provided by the Alaska Power Authority, the Kodiak Electric Association, and the ADF&G. Research in Southwest Kodiak was funded by the U.S. Fish and Wildlife Service (USFWS). We sincerely appreciate assistance received from numerous employees of the ADF&G and USFWS throughout all phases of these projects. J.A. Patterson, M. Vivion, T. Chatto, V. Lofstedt and C. Lofstedt, and several other pilots, provided expert flying skills. Susan Malutin was a valued assistant throughout the projects, with her clerical skills and constant moral support.

STUDY AREA

The Kodiak archipelago is located in the Gulf of Alaska, approximately 400 km southwest of the city of Anchorage, Alaska (Fig. 1). Kodiak Island is the largest island in the archipelago, encompassing 9,600 km^2. The region has a maritime climate characterized by cloudy skies, cool temperatures, moderate to heavy precipitation, and frequent windstorms. Maximum temperatures generally range from 13-18 C and winter temperatures below -6 C are infrequent. Annual precipitation at Kodiak city averages 157 cm, and occurs primarily as rain near sea level and snow in the higher elevations from October to May. In general, the southwest portion of the island has warmer summers, cooler winters and less precipitation than the northern part. The archipelago supports a human population of 14,000, most of whom live in the city of Kodiak and 6 outlying villages.

The Terror Lake study area includes 774 km^2 on the northern portion of Kodiak Island. Inland topography varies from rolling hills and gentle valleys to steeply ascending ridges and peaks to elevations of 1,340 m along tributaries into Kizhuyak and Terror Bays. Vegetation varies from marine aquatics in the bays to hillsides covered with dense shrub thickets interspersed with meadows (Smith and Van Daele 1990.) Alpine vegeta-

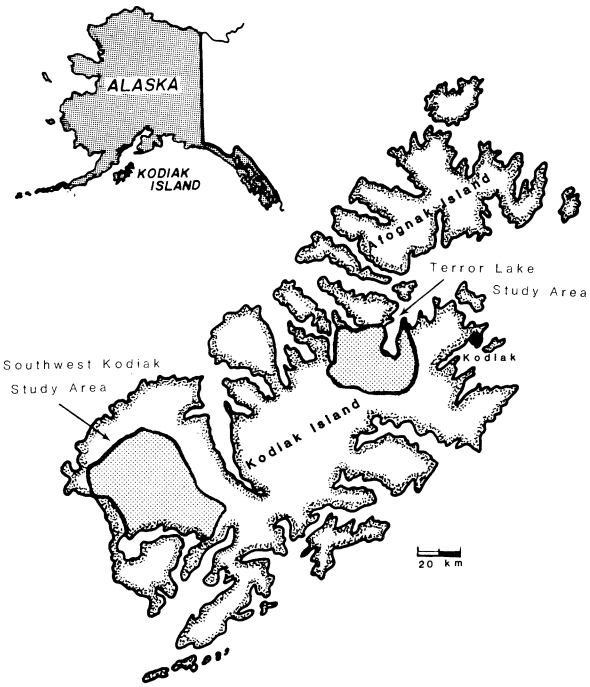

Fig. 1. Location of Terror Lake and Southwest Kodiak brown bear study areas, Kodiak Island, Alaska.

tion includes low willow (*Salix* spp.), sedges (*Carex* spp.), and ericaceous heath. Salmon are abundant throughout the summer with pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and coho salmon (*O. kisutch*) being most common.

The Southwest Kodiak study area encompasses 1,231 km^2 between Uyak, Deadman and Olga Bays. The topography is typified by wide flat valleys, rolling foothills, and occasional areas of steep terrain. The highest peak (997 m) and the most rugged terrain occur in the southeast portion of the study area. Lowlands support a mosaic of willow and herbaceous cover, with drier sites dominated by heath vegetation (Barnes 1990.) Vegetation on mid-elevation slopes is similar to that in the Terror Lake area, but shrub thickets are not as extensive. Alpine vegetation is similar to that found in the Terror Lake area, but is less extensive. Salmon are abundant from June through October, and occur in greater numbers and over a larger percentage of this study area than in the Terror Lake area. Sockeye (*O. nerka*), chinook (*O. tshawytscha*), coho, pink, and chum salmon all occur in this area.

Brown bear densities were similar in both areas (1 bear/2.9 km^2 at Terror Lake and 1 bear/3.5 km^2 in Southwest Kodiak) (Barnes et al. 1988), but home range sizes were considerably different. At Terror Lake, the average annual home range size for radio-collared female and male bears was 28 km^2 and 133 km^2, respectively (Smith and Van Daele 1988). In Southwest Kodiak, the average annual home range size for radio-collared female and male bears was 92 km^2 and 219 km^2, respectively (Barnes 1990). No bears were known to have used both study areas.

METHODS

Data on denning chronology, den locations and bear reproductive status were collected during weekly radio-tracking flights from April through December and monthly flights from January through March. Den entrance dates were estimated to be the midpoint between the last date a bear was known to be out of its den and 1st date it was known to be in its den. When the period between relocation flights exceeded 20 days, den entrance dates were not calculated. Emergence dates were estimated to be at the midpoint between the date of the last flight that a bear was closely associated with its den and the date of the 1st flight it was no longer associated with its den. Close association was considered to be daily use of the den itself. Mean denning periods were calculated by averaging the maximum and minimum number of days in the den. Maximum denning periods were the interval between the last date a bear was seen out of its den and the 1st date it was seen away from its den. Minimum denning periods were the interval between the 1st date a bear was known to be in its den and the last date it was known to be in its den. Mean denning periods were not calculated for bears that had a range of more than 40 days between the minimum and maximum denning periods.

Estimated slope categories (flat, gentle: <30%, moderate: 30-45%, steep: >45%), aspects (8 categories based on true bearing), vegetative cover and den locations were recorded in the field. Elevation and distance data were derived from U.S. Geological Survey 1:63,360 topographic maps. Den sites were categorized into 1 of 3 habitat categories (alpine, midslope, lowland) based on elevation and vegetation characteristics within 1 ha of the site. Den construction data were collected during ground visits to selected dens during the summer. Statistical comparisons of denning chronologies and den site characteristics between the 2 study areas and among reproductive categories (male, lone female, female with cubs-of-the-year [COY], and females with cubs ≥1 yr) were accomplished with analysis of variance tests, *t*-tests, Bonferroni *z*-tests and chi-squared contingency tests. Denning chronology was also analyzed by comparing the percentage of radio-collared bears within the various reproductive categories that were known to be in dens by certain dates. The reproductive status was determined

Table 1. Mean den entrance dates for radio-collared brown bears, by reproductive category, in 2 study areas on Kodiak Island, Alaska, 1982-1988.

Study area	Reproductive category	Mean den entrance date	Range[a]	Sample size	Standard deviation
Terror Lake	Male	16 November	4 Nov.-14 Dec.	4	18.9
	Lone female[b]	10 November	21 Oct.-2 Jan.	40	14.9
	Female w/young	9 November	23 Oct.-14 Dec.	36	13.1
	Pregnant female	5 November	15 Oct.-28 Nov.	27	11.2
Southwest Kodiak	Male	12 December	3 Dec.-21 Dec.	2	12.7
	Lone female[b]	26 November	22 Oct.-20 Dec.	12	18.9
	Female w/young	3 December	17 Oct.-19 Jan.	47	21.9
	Pregnant female	19 November	19 Oct.-29 Dec.	10	27.2

[a] Range of estimated entrance dates.
[b] May include some pregnant females that lost their newborn cubs prior to the 1st post-denning observation in the spring.

each spring at emergence. Some pregnant females may have lost their newborn cubs prior to our 1st post-denning observations, and could have been misclassified as "lone females".

RESULTS

One hundred and fifteen radio-collared brown bears (94 females and 21 males) were located in 321 dens (293 occupied by females and 28 by males). There were 184 dens (57%) used by 64 bears at Terror Lake, and 137 dens (43%) used by 51 bears in Southwest Kodiak.

Denning Chronology

Typical denning behavior consisted of periods of excavation activity interspersed with extended rest periods. Bears often made several excavations in adjacent locations prior to completing a den.

Bears at Terror Lake generally moved into denning areas by mid- to late October. In Southwest Kodiak, bears did not exhibit obvious movements into identifiable denning areas, and they entered dens later ($P < 0.1$) than bears at Terror Lake (Table 1). These differences were significant ($P < 0.1$) for all female reproductive categories, averaging 13.7 days difference for pregnant females, 17.4 days for lone females, and 24.6 days for females with young. Sample sizes were insufficient to test differences between the mean den entrance dates of males. Den entrance dates in both areas were later than have been reported in other brown bear populations in Alaska (Schoen et al. 1987, Miller 1990)(Table 2).

In most cases, females entered dens earlier than did males. Pregnant females generally entered dens earlier than lone females or females with young (Fig. 2). Pregnant females had an earlier mean entrance date than did females with young in both study areas; however, these differences were not statistically significant.

Den emergence in both study areas generally began in early April, although a few individuals left their dens as early as February. A typical pattern of emergence consisted of: 1) opening the den entrance; 2) remaining near or in the den for several days, interspersed with short forays in the immediate den vicinity; and, 3) abandonment of the den site (emergence). Chronology of emergence was generally the reverse of entrance chronology, with males emerging 1st, followed by lone females and females with yearling and older offspring. Females with COY were usually the last group to emerge (Fig. 3). Mean emergence dates of females differed ($P < 0.1$) among all reproductive categories at Terror Lake (Table 3). In Southwest Kodiak, females with COY emerged later than other females ($P < 0.1$), but emergence dates were similar for lone females and females with older offspring ($P > 0.2$). Bears in Southwest Kodiak appeared to emerge somewhat earlier than their counterparts at Terror Lake

Table 2. Mean den entrance dates for radio-collared brown bears in 4 separate study areas in Alaska.

Study area	Reproductive status			
	Males	Lone females	Females with young	Pregnant females
Southcentral Alaska[a]	16 Oct	14 Oct	15 Oct	13 Oct
Southeastern Alaska[b]	5 Nov (20)[c]	5 Nov (22)[c]	27 Oct (12)[c]	22 Oct (9)[c]
Terror Lake, Kodiak	16 Nov (31)	10 Nov (27)	9 Nov (25)	5 Nov (23)
Southwest Kodiak	12 Dec (58)	26 Nov (43)	3 Dec (50)	19 Nov (37)

[a] Miller (1990); females with 2-year-olds included in the "lone female" category.
[b] Schoen et al. (1987).
[c] Numbers in parentheses indicate the difference, in days, from the mean den entrance dates of bears in similar reproductive categories in southcentral Alaska.

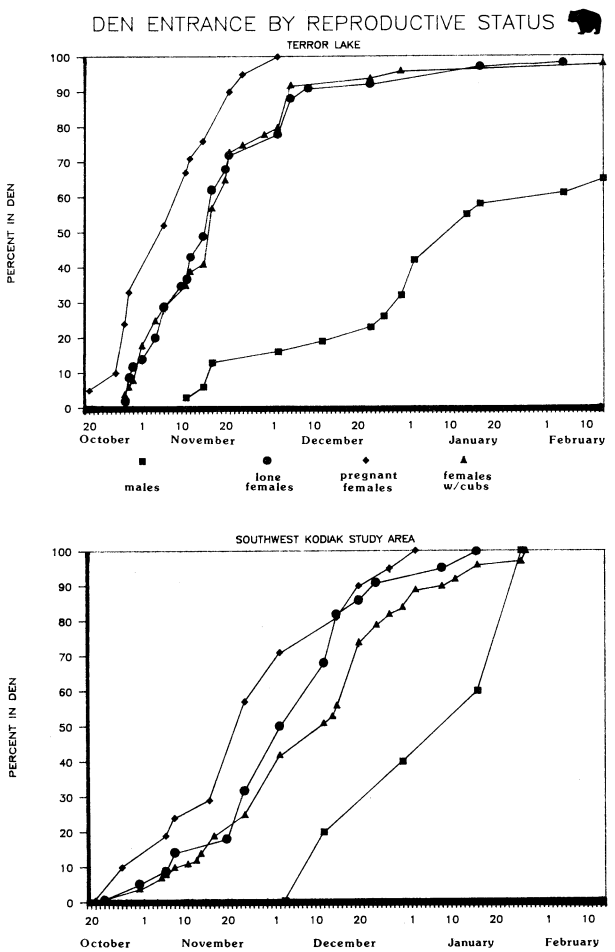

Fig. 2. Chronology of den entrance by radio-collared brown bears in each reproductive category in 2 study areas on Kodiak Island, Alaska, 1982-1988.

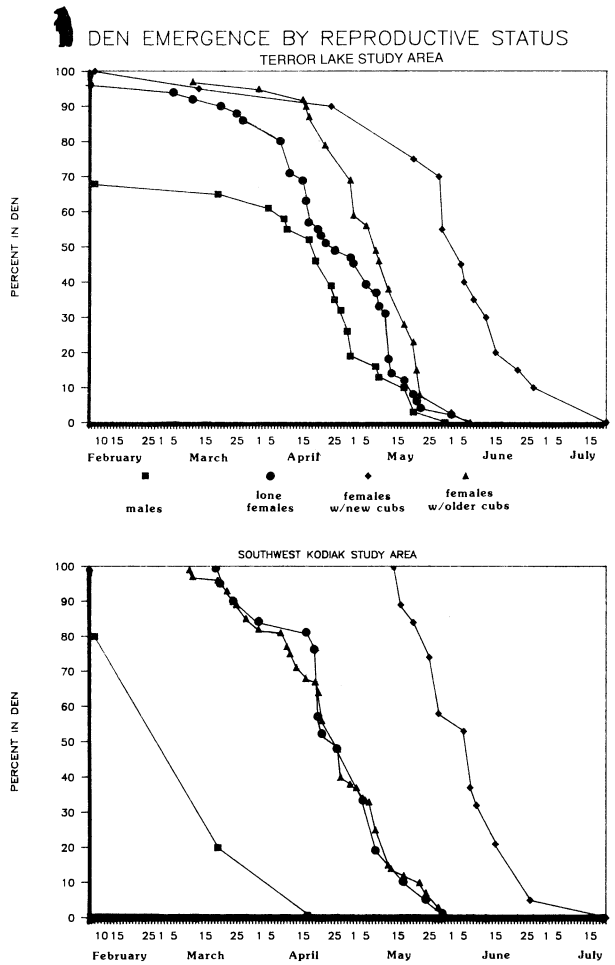

Fig. 3. Chronology of den emergence by radio-collared brown bears in 2 study areas on Kodiak Island, Alaska, 1982-1988.

(Fig. 3), but these differences were not statistically significant. Den emergence dates in both areas were similar to those reported from other brown bear populations in Alaska (Schoen et al. 1987, Miller 1990)(Table 4).

Males had the shortest mean denning period (135 days) and females with COY had the longest (205 days). Bears in all reproductive categories in both study areas had different mean denning periods ($P < 0.05$), with the exception of lone females compared to females that emerged with yearling or older offspring. At Terror Lake, lone females and females with yearling or older offspring were still different but at a slightly lower level of significance ($0.1 > P > 0.05$), and in the Southwest area females in these reproductive categories did not have significantly different denning periods ($P > 0.2$). Males ($P < 0.01$), lone females ($P < 0.05$), and females that emerged with yearling or older offspring ($P < 0.01$) stayed in their dens longer in the Terror Lake study area than in the Southwest Kodiak study area ($P < 0.1$)(Table 5). Females that emerged with COY did not have different mean denning periods between the 2 areas ($P > 0.2$).

Den entrance and emergence dates appeared to vary annually in both study areas, but data were insufficient to analyze these differences objectively.

Den Site Characteristics

Fifty-six percent ($n = 178$) of the dens were in the alpine habitat category, 43% ($n = 139$) in the midslope category, and 2% ($n = 3$) in the lowland category. One den was not located accurately enough to assign it to a specific category. Radio-collared bears at Terror Lake occupied dens in alpine areas more frequently than did the bears in Southwest Kodiak ($P < 0.1$). The relative availability of each habitat type in each study area ex-

Table 3. Mean den emergence dates for radio-collared brown bears in 2 study areas on Kodiak Island, Alaska, 1982-1988.

Study area	Reproductive category[a]	Mean den entrance date	Range[b]	Sample size	Standard deviation
Terror Lake	Male	22 April	31 Mar.-24 May	18	13.5
	Lone female	2 May	23 Mar.-7 Jun.	36	18.5
	Female w/young	12 May	31 Mar.-7 Jun.	31	15.9
	Female w/coy	27 May	20 Mar.-13 Jul.	15	27.1
Southwest Kodiak	Male	8 March	1 Feb.-11 Apr.	2	48.8
	Lone female	28 April	22 Mar.-22 May	14	17.8
	Female w/young	27 April	11 Mar.-8 Jun.	61	20.3
	Female w/coy	31 May	7 May-3 Jul.	18	15.6

[a] Based on 1st observation after emergence; the "Lone female" category may include some pregnant females that lost their newborn cubs prior to our 1st post-denning observation; "Female w/young" were those known to have emerged with yearling or older cubs, females that entered with cubs but emerged alone were excluded from this analysis; "Females w/coy" were those that were known to have emerged with cubs-of-the-year.
[b] Range of estimated emergence dates.

plained some of the variation ($P < 0.01$), but individual preference also appeared to play a role in den site selection (Table 6). In both areas, dens were located in lowlands less often than would be expected based on availability ($P < 0.01$). In the Terror Lake area, midslopes were used about equal to their availability ($P > 0.1$), and dens were located in alpine areas more often than would be expected ($P < 0.1$). Conversely, in Southwest Kodiak, alpine areas were used about equal to their availability ($P > 0.1$), and dens were located in midslope areas more often than would be expected ($P < 0.1$). These differences were also reflected in the mean den elevations in the 2 areas. At Terror Lake, dens ranged from 91 to 1,189 m, with a mean of 665 m. In Southwest Kodiak, dens ranged from 128 m to 915 m, and with a mean elevation of 457 m. Mean den elevations varied annually and by sex, but no consistent trends were evident.

Fifty-two percent ($n = 167$) of the dens were located on steep slopes, 40% ($n = 127$) on moderate slopes, 8% ($n = 26$) on gentle slopes, while no dens were found on flat sites. Dens were found on steep slopes more often ($P < 0.1$) at Terror Lake (65%)($n = 120$) than in Southwest Kodiak (35%)($n = 47$). Of those dens located on moderate or gentle slopes at Terror Lake, 80% (51/64) were associated with cliffs or rock outcrops. This association with cliffs or rock outcrops on moderate and gentle slopes suggests that these microhabitats were equivalent to steep slopes for meeting denning requirements. If this was the case, 93% (171/184) of the dens at Terror Lake were in steep microhabitats. In contrast, only 11% of the dens in Southwest Kodiak that were on gentle or moderate slopes were associated with cliffs or rock outcrops, resulting in a total of only 32% (43/136) of the den sites in steep microhabitats.

Aspects of den sites were variable and apparently not a critical factor in determining suitability of a den site. Den aspects differed between the 2 areas ($P < 0.1$). Northerly aspects (north, northeast, and northwest) were most frequently used for dens (33%) at Terror Lake, while in Southwestern Kodiak northerly aspects were the least frequently used (20%)(Table 7). We collected no data on the relative availability of various slopes and aspects in the 2 areas.

Gross den construction characteristics were determined for 135 dens, including: 111 excavated dens (15 in Terror Lake and 96 in Southwest); 17 natural rock cavities (3 in Terror Lake and 14 in Southwest); 5 snow dens (all in Terror Lake area); and, 2 snow dens in rock cavities (both in Terror Lake area). Den dimensions and structure were variable, and similar to those reported in other

Table 4. Mean den emergence dates for radio-collared brown bears in 4 separate study areas in Alaska.

Study area	Reproductive status[a]			
	Males	Lone females	Females with young[b]	Females with coy[c]
Southcentral Alaska[d]	23 Apr.	30 Apr.	4 May	15 May
Southeastern Alaska[e]	19 Apr.	29 Apr.	16 May	11 May
Terror Lake, Kodiak	22 Apr.	2 May	12 May	27 May
Southwest Kodiak	8 Mar.	28 Apr.	27 Apr.	31 May

[a] Determined at 1st post-denning observation.
[b] Females with yearling or older offspring.
[c] Females with cubs-of-the-year.
[d] Miller (1990); females with 2-year-olds included in the "lone female" category.
[e] Schoen et al. (1987).

Table 5. Average denning periods of radio-collared brown bears in each reproductive category in 2 study areas on Kodiak Island, Alaska, 1982-1988.

Study area	Mean denning period in days(sample size in parentheses)			
	Males	Lone females[a]	Females with young[b]	Females with coy[c]
Terror Lake	157 (6)	176 (31)	187 (20)	211 (15)
Southwest Kodiak	91 (3)	160 (9)	149 (41)	198 (12)
Kodiak total	135 (9)	172 (40)	162 (61)	205 (27)

[a] The "Lone female" category may include some pregnant females that lost their newborn cubs prior to our 1st post-denning observation.
[b] Females known to have emerged with yearling or older cubs; females that entered with offspring but emerged alone were excluded from this analysis.
[c] Females known to have emerged with cubs-of-the-year.

Table 6. Relative distribution of den locations by habitat category for radio-collared brown bears in 2 study areas on Kodiak Island, Alaska, 1982-1988.

Study area[a]	Habitat category			Total
	Lowland	Midslope	Alpine	
Terror Lake				
% Area (km²)	26.6 (206)	33.1 (256)	40.3 (312)	774 km²
% Den sites (*n*)	1.7 (3)	26.8 (48)	71.5 (128)	179 dens
Southwest Kodiak				
% Area (km²)	40.6 (500)	36.6 (451)	22.8 (281)	1,231 km²
% Den sites (*n*)	0.0 (0)	73.9 (85)	26.1 (30)	115 den

[a] Includes only the area (km²) and the dens that were within the core study areas; bears which had home ranges within our study areas but denned outside of the areas were excluded from this analysis.

investigations of brown bear dens in Alaska (Lentfer et al. 1972, Schoen et al. 1987, Miller 1990).

Den characteristics (elevation, aspect, construction) of bears in various reproductive categories varied annually in both areas. These variations were not consistent and, because of data and sample size limitations, we could not correlate them with weather or reproductive status of the bear.

Den Concentrations

High concentrations of dens were found at 2 locations in the Terror Lake area: Den Mountain and Baumann Creek. The 2 areas combined comprised only 1% (7.8 km²) of the Terror Lake area, but they contained 36% (67/184) of the dens of radio-collared bears, including 40% (64/161) of the dens of females and 13% (3/23) of the dens of males. No comparable concentrations were observed in Southwest Kodiak.

Den Mountain is a 1,119 m glaciated peak about 2 km north of Terror River. Most dens were located on steep tundra slopes and barren rock escarpments in north- and west-oriented cirques. Most dens appeared to be excavated, although some natural cavities were used. Thirty-seven dens of 10 radio-collared bears were located on Den Mountain during this study, 95% (35) were occupied by females. These females rarely ventured further than 10 km from Den Mountain. Both males that denned in the area were less than 5 years old and vacated the area soon after emergence. Unmarked bears exhibiting denning behavior were also observed in the area.

The middle reaches of Baumann Creek flow through a narrow valley approximately 150-180 m in elevation, bordered by steep, shrub-covered sides to 610 m. Thirty dens of 9 radio-collared bears were located in this area, 97% (29) were occupied by females. Movements of these females were generally within 10 km of the Baumann Creek concentration area. Numerous unmarked bears were also observed denning in this area. Although the dense vegetation and the fractured, rocky terrain often precluded close observation of actual den sites, the use of natural rock cavities for dens appeared to be greater in the Baumann Creek area than in other areas.

Fidelity to Den Sites

Individual bears exhibited fidelity to specific den sites in both study areas. Data on successive years' den use

Table 7. Aspects of dens used by radio-collared brown bears in 2 study areas on Kodiak Island, Alaska, 1982-1988 (percent in parentheses).

Study area	Aspect								Total
	North	Northeast	East	Southeast	South	Southwest	West	Northwest	
Terror Lake	43 (23)	35 (19)	14 (8)	12 (7)	22 (12)	29 (16)	17 (9)	12 (7)	184
Southwest Kodiak	8 (6)	21 (15)	12 (9)	24 (18)	14 (10)	21 (15)	23 (17)	13 (10)	136
Total	51 (16)	56 (18)	26 (8)	36 (11)	50 (16)	40 (13)	25 (13)	25 (8)	320

were collected for 74 radio-collared bears using 162 dens. Eighty (49%) of these dens were less than 1 km apart in successive years. Females occupied the same den site during 2 successive seasons in 29 of these instances (8 in Terror Lake and 21 in Southwest). Actual use of the same den was suspected in all cases, but could not always be confirmed. Two females used their same den site for 5 consecutive winters. Fifty-three (33%) of the dens were 1 to 3 km apart and 29 (18%) were more than 3 km apart in successive years. The mean distance between individual dens in successive years was 1.9 km (range = 0.0 - 25.7 km). Males exhibited less fidelity to den sites ($\bar{x}$ = 7.8 km; n = 5; range = 1.3 - 20.0 km) than did females ($\bar{x}$ = 1.7 km; n = 157; range = 0.0 - 25.7 km)($P < 0.01$). Mean distance between successive dens used by individual female bears was similar in the 2 study areas. Sample sizes were inadequate to test differences among males.

Radio-collared bears occupying Den Mountain exhibited high fidelity to den sites. Seventy-four percent (20/27) of the dens of radio-collared bears in this area were within 1 km of the den used during the previous year. The mean distance between dens of individual females in successive years was 1.0 km (n = 25; range = 0.0-9.2 km). Female bears denning near Baumann Creek also exhibited high fidelity to previously used den sites throughout the study period ($\bar{x}$ = 1.6 km; n = 18; range = 0.0-2.7 km).

Denning Anomalies

Thirty-five radio-collared bears did not conform to the conventional denning pattern of entering a single winter den and remaining in that den throughout the winter. Included were 27 females (33 instances) that used multiple dens during a single winter, and 7 males and 1 female (12 instances) that did not occupy dens during at least 1 winter.

Of the females that used multiple dens in a single season, 31 cases involved the use of 2 dens, and 2 cases involved the use of 3 dens. No males exhibited this behavior. Twenty-one cases occurred at Terror Lake and 12 in Southwest Kodiak. At Terror Lake, females that used only 1 den during a season occupied dens at higher elevations ($P < 0.1$) ($\bar{x}$ = 694 m) than the initial dens of females that moved dens within a season ($\bar{x}$ = 579 m). This difference was not evident in Southwest Kodiak.

Characteristics of 1st and 2nd den sites were not conspicuously different. Mean elevations of 2nd den sites (631 m in Terror Lake and 456 m in Southwest) were somewhat higher than elevations of 1st den sites (579 m in Terror Lake and 424 m in Southwest), but this difference was not statistically significant ($P > 0.1$) in either area. Aspects and slopes of 1st and 2nd den sites were similar in both areas. Mean distance between 1st and 2nd den sites at Terror Lake was 1.5 km and distances ranged from 0.3 km to 8.9 km. In the Southwest area the mean distance was 1.2 km (range = 0.3-2.9 km). The mean distance between 2nd and 3rd dens was 0.8 km (range = 0.6-1.0; n = 2); both of these cases were in Southwest Kodiak.

Thirty-six percent (12) of these den changes involved single (possibly pregnant) females or females that emerged with COY, and 63% (21) involved females with yearling or older offspring. In Southwest Kodiak, 42% (5/12) of the cases involved sows that emerged with 3-year-olds. Overall, no bears changed dens in 1982/83, 1 in 1983/84, 6 in 1984/85, 17 in 1985/86, 8 in 1986/87, and 1 in 1987/88. In most cases, we were not able to determine accurately when bears moved between dens.

Seven males (11 instances) apparently did not den during at least 1 of the winters that they were monitored. These represented 22% (7/32) of the individual males and 28% (11/39) of the denning periods for males monitored during the study. All instances occurred at Terror Lake, although 1 male in Southwest Kodiak may have used a temporary den for only a short time. The frequency of non-denning did not appear to vary annually. Three cases occurred in 1982/83 and in 1983/84, 2 in 1984/85 and in 1986/87, and 1 in 1985/86. One bear did not den for the 3 consecutive years he was monitored, 2 did not den for 2 consecutive years, and 4 were monitored during only 1 denning season. Sequential radio-locations of the non-denning males indicated they were relatively sedentary in mid-winter, making relatively short movements and appearing somewhat lethargic. One bear seen bedded under a small spruce (*Picea sitchensis*) did not awaken despite repeated close passes with a fixed-wing aircraft.

The only female that did not den lost her COY's in October 1985 within her traditional home range near Baumann Creek. She spent the winter near the village of Port Lions, several kilometers from her previous home range, where residents observed her foraging in the village landfill. She was found dead in May 1986 within 1 km of the landfill. Cause of death could not be determined, but she appeared to be emaciated and had little subcutaneous fat.

Mortality at Den Sites

Four radio-collared bears, all females, died at or near their den sites. All occurred at Terror Lake; 2 in 1984/85 and 2 in 1985/86. Two cases involved females with COY (0.9 yr), and 2 involved single (possibly pregnant) females. Direct causes of mortality could not be determined.

DISCUSSION

Winter dormancy is a complex behavioral and physiological adaptation in response to the decreased food availability and winter weather. Although numerous authors have described denning characteristics, knowledge of what factors dictate when or where a bear will den is incomplete. Our investigation on Kodiak provided additional information, but even with a large sample of bears, we did not provide any specific answers as to what makes bears enter dens or what is "critical brown bear denning habitat". We found that subpopulations of bears living within 70 km of each other on the same island, with no real physical barriers to movement, had developed noticeably different denning behaviors.

The relative order in which bears in various reproductive categories entered dens was similar in both study areas. Females entered dens earlier than most males, and pregnant females frequently entered dens earlier than other bears. Onset of den entrance in both areas was gradual and not related to the 1st heavy snowfall, as has been reported in the Yellowstone ecosystem (Craighead and Craighead 1972).

We found a marked difference in mean den entrance dates between the 2 study areas. Females in Southwest Kodiak generally entered dens 2 to 3 weeks later than their counterparts at Terror Lake. We hypothesize that this variation is directly related to the differences in food availability between the 2 areas during late autumn (mid-October through mid-December). In the Terror Lake area, major sources of bear food were depleted by late autumn. Herbaceous vegetation was desiccated, and berries were no longer abundant. A few salmon were available until December, but most had finished spawning and had been washed to the sea by mid-October. A different scenario occurred in Southwest Kodiak during that same time period (Barnes 1990). Sockeye salmon, a species uncommon in the Terror Lake area, were still actively spawning along the shores of the major lakes and coho salmon were readily available in several streams in Southwest Kodiak until mid-December.

Johnson and Pelton (1980) reported considerable variation in the denning periods of black bears (*U. americanus*) across their range in North America with a trend toward longer denning periods in more northerly latitudes. These variations resulted principally from differences in the time of den entrance, and they suggested that this was a result of harsher climates and limited food availability in the northern areas. A similar pattern was also evident among brown bear populations in southern portions of Alaska (Schoen et al. 1987, Miller 1990, this study). Although it is risky to make generalizations based on "average bears" in "average years", a consistent pattern of den entrance chronology is apparent. Bears in southcentral Alaska, with the least available food and the coldest temperatures in late autumn, entered dens earlier than bears in areas characterized by milder conditions. Southeast Alaska and Kodiak have similar winter climates, however late autumn food availability is different. Southeast Alaska has the lowest relative food availability in the late autumn and the earliest mean entrance dates, while Southwest Kodiak has the greatest relative availability of late autumn food and the latest mean entrance dates.

The relative timing of den emergence on Kodiak followed a pattern similar to that reported for brown/grizzly bear populations in other parts of Alaska (Schoen et al. 1987, Miller 1990), in the Yellowstone ecosystem (Judd et al. 1986), in Montana (Servheen and Klaver 1983), and in Siberia (Kistchinski 1972). Males were generally the 1st group to vacate their dens, and females with COY were usually the last. Comparison of mean den emergence dates reported for bears in 4 areas of southern Alaska (Schoen et al. 1987, Miller 1990, this study) revealed no consistent patterns similar to those noted for den entrance chronology. On Kodiak, there appeared to be a tendency for bears to emerge earlier on the southern part of the island than in the northern part, but the difference was not significant. Weather patterns and food availability may influence den emergence patterns in southern portions of Alaska, but not to the same degree that they influence den entrance patterns.

Snow retention characteristics are considered to be a critical factor at grizzly bear denning sites in the Rocky Mountains (Craighead and Craighead 1972, Vroom et al. 1980, Servheen and Klaver 1983). Lentfer et al. (1972) also cited snow cover as an important factor on Kodiak Island. Although most of the dens at Terror Lake were snow-covered throughout the denning period, bears did not appear to seek out sites that had greater snow depths. In Southwest Kodiak, it was not uncommon for den sites to have little snow cover (<1 m) throughout winter, and for some den entrances to remain open all winter. Schoen et al. (1987) reported den site characteristics on Admiralty Island in southeastern Alaska similar to those observed at Terror Lake. They speculated that snow was probably less important for insulation in south-coastal Alaska, where winter temperatures rarely fell below –20 C, than in colder interior areas. They suggested that bears needed dry, cold sites where temperatures generally remained below freezing and surface water was rare. That hypothesis is consistent with our findings on Kodiak.

Most dens were apparently excavated into hillsides or under rock outcrops. Bears frequently dug in several places prior to excavating their final den. Some of these exploratory diggings may have been day beds, but most appeared to be aborted denning attempts, possibly abandoned because of inadequate soil conditions. Soil depth and stability appeared to be critical factors for denning in most cases; however, snow dens and natural cavities in rock formations were not uncommon.

Den site characteristics were remarkably different between the 2 Kodiak study areas. Bears in the Terror Lake area preferred steep slopes in alpine habitat for dens. Winter temperatures at low and middle elevations are milder and rain is more common in that area than in Southwest Kodiak. Bears at Terror Lake may prefer alpine areas for dens because they are high enough that soils remain frozen throughout the winter at the higher elevations. Terror Lake alpine habitat is characterized by steep, rocky crags with numerous natural fissures and cavities. These crags are commonly surrounded by steep slopes that are well-drained and covered with sedges and ericaceous shrubs. The substrate is usually deep enough to dig a den and, when frozen, stable enough for a den to retain its integrity throughout the winter. Alpine areas in Southwest Kodiak had vegetation and soil characteristics that resembled those found at Terror Lake, but the topography was gentler and there were fewer rock outcrops.

In Southwest Kodiak, midslope habitat and moderate slopes were preferred denning sites. Midslope habitats in Southwest Kodiak are usually on hillsides with slope >30° that are vegetated with a mosaic of herbaceous meadows and scattered alder thickets. We believe they provided an ecological equivalent of the steep alpine slopes found in the Terror Lake area. Most of the dens found in midslope habitat were within or at the edge of alder thickets. Alder root systems are probably necessary to stabilize dens excavated in loose, unfrozen soils (Lentfer et al. 1972). The relatively cooler, drier winter climate, coupled with the later den entrance dates, may also give the bears in the Southwest area more flexibility in selection of a dry den site with stable soils.

The difference in den site characteristics between the 2 areas is especially interesting because of their proximity. We suspect that because bears in both areas occupied small annual home ranges, they utilized the most suitable denning habitat available within their home range. Suitable den sites were those sites that remained dry throughout the denning period, and provided adequate soil depth and stability for excavation of a den, or a suitable natural cavity.

Adaptability in selection of sites was apparent even within the Terror Lake area. Den concentrations at Den Mountain and Baumann Creek were in conspicuously different habitats. Female bears were able to satisfy all of their needs in small areas in northern Kodiak, and they usually occupied relatively small annual home ranges. Sites such as Den Mountain and Baumann Creek may offer the best den site characteristics within the home ranges of several bears and thus have disproportionately heavy use. Learned behavior may also play a part in den site selection by females. Subadult females often remain in the vicinity of their mother's home range, whereas male offspring frequently disperse (Reynolds et al. 1987, Miller 1987). The combination of high bear density together with learned behavior may result in large numbers of females using the same denning area.

Although the "average" bear can successfully den in a variety of sites, the high degree of fidelity to specific den sites exhibited by individual brown bears on Kodiak suggests a preference for certain site characteristics and/or that tradition plays a major role in den selection. Mean distances between dens of individual females in successive years were considerably less in the Kodiak study areas (1.7 km) than were observed in southeastern Alaska (3.5 km; Schoen et al. 1987) or in southcentral Alaska (6.1 km; Miller 1990).

Two notable anomalies in denning behavior were observed in this study; use of multiple dens and failure to enter dens. We found little evidence that maternal status or cub age was related to the use of multiple dens. Second dens were usually at higher elevations than 1st dens, but site characteristics and locations were similar. We could not accurately determine the timing of, or the reasons for, movements to 2nd dens in most cases. Most of the movements at Terror Lake appeared to coincide with unseasonable warm and wet late autumn/early winter periods. Some flooding of dens probably occurred during these periods, which led to abandonment. This relationship between weather conditions and movement to a 2nd den was not apparent in Southwest Kodiak.

The failure of some males to den did not appear to be affected by interannual variations in food availability or weather conditions. Some males were active throughout the winter during every year of the study. More than 25% of the radio-collared males at Terror Lake did not den during at least 1 of the winters of the study. It is not uncommon to see bear tracks throughout the winter months on the Kodiak archipelago. We found no published reports of non-denning brown/grizzly bears, but non-denning black bears have been reported in Virginia and North Carolina (Hellgren and Vaughan 1987). The relatively warm winter climate and long seasonal availa-

bility of food probably allow some bears to remain active for longer periods of time on Kodiak compared to other portions of brown/grizzly bear range. Non-denning bears apparently spent much of their time bedded in shrub or spruce microhabitats and intermittently traveled relatively short distances within their normal home ranges. Although these bears never entered dens, their behavior appeared to be similar to the "walking hibernation" described by Nelson et al. (1983) for bears that had recently emerged from hibernation. No data on winter feeding were collected during this study, but it is suspected that non-denning bears reduced their food intake and may have experienced lowered metabolism periodically.

MANAGEMENT IMPLICATIONS

Responsible management of a bear population requires an understanding of the denning ecology of the population. Harvest rates and percentage of females in the harvest can be affected by the timing of bear hunting seasons in relation to denning chronology. Knowledge of suitable denning habitat and den concentration areas is critical to evaluation of potential effects of human activities and developments on the bear population.

On Kodiak Island, hunters harvest approximately 5.4% of the total bear population annually (ADF&G files). The fall hunting season (25 October - 30 November) coincides with the peak period of den entrance, and the spring hunting season (1 April - 15 May) coincides with the onset of den emergence. A limited number of permits are issued to non-guided (Alaska residents) and guided (non-resident) hunters. Bears of either sex are legal game, but cubs and females accompanied by cubs may not be taken.

By the close of the fall hunting season, approximately 77% of the lone females and 98% of the pregnant females at Terror Lake are in dens. In contrast, only about 40% of the lone females and 70% of the pregnant females in Southwest Kodiak have entered dens by that time. This suggests that females in Southwest Kodiak are more available to hunters in the fall than are females in the Terror Lake area. The relative vulnerability of females in Southwest Kodiak is enhanced by their frequent use of salmon streams during the fall hunting season, and by their use of denning habitat that is more accessible to humans (i.e., midslope habitats). This differential vulnerability must be taken into account when analyzing harvest data and when recommending hunting seasons. Females are probably equally vulnerable during the spring hunting season because emergence patterns are similar in the 2 areas.

The danger of extrapolating data from a denning study in 1 area to characterize denning habitat in another was evidenced in a report which predicted the impacts of the Terror Lake hydroelectric project on brown bears (Spencer and Hensel 1980). In their assessment, Spencer and Hensel delineated a "usable denning habitat zone" using information collected from southern Kodiak Island (Troyer and Hensel 1969, Lentfer et al. 1972). This zone included most of the mid-elevation (150 m to about 600 m) shrub habitat in the Terror Lake area and did not encompass most of the alpine areas. Less than 40% of the dens of radio-collared bears were within the "usable denning habitat" zone, and the den concentration area on Den Mountain was not included in the zone. Fortunately, the impacts of the hydroelectric project on denning were not as great as those predicted in the pre-project assessment because most of the impacts were in the lowland and midslope areas (Smith and Van Daele 1990). However, the error can serve as a valuable lesson that caution should be exercised when defining "critical denning habitat" for any segment of the bear population.

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