GRIZZLY BEAR DENNING CHRONOLOGY AND MOVEMENTS IN THE GREATER YELLOWSTONE ECOSYSTEM

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Abstract: Den entrance and emergence dates of grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem are important to management agencies that wish to minimize impacts of human activities on bears. Current estimates for grizzly bear denning events use data that were collected from 1975–80. We update these estimates by including data obtained from 1981–99. We used aerial telemetry data to estimate week of den entry and emergence by determining the midpoint between the last known active date and the first known date denned, as well as the last known date denned and the first known active date. We also investigated post emergence movement patterns relative to den locations. Mean earliest and latest week of den entry and emergence were also determined. Den entry for females began during the fourth week in September, with 90% denned by the fourth week of November. Earliest den entry for males occurred during the second week of October, with 90% denned by the second week of December. Mean week of den entry for known pregnant females was earlier than males. Earliest week of den entry for known pregnant females was earlier than other females and males. Earliest den emergence for males occurred during the first week of February, with 90% of males out of dens by the fourth week of April. Earliest den emergence for females occurred during the third week of March; by the first week of May, 90% of females had emerged. Male bears emerged from dens earlier than females. Denning period differed among classes and averaged 171 days for females that emerged from dens with cubs, 151 days for other females, and 131 days for males. Known pregnant females tended to den at higher elevations and, following emergence, remained at higher elevation until late May. Females with cubs remained relatively close (<3 km) to den sites until the last 2 weeks in May. Timing of denning events was similar to previous estimates for this and other grizzly bear populations in the southern Rocky Mountains.

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Denning behavior in bears has been described as an elaborate bedding process that probably evolved in response to adverse environmental conditions, primarily seasonal lack of food and unfavorable weather (Mystrud 1983). Nelson and Beck (1984) separated the physiological aspects of denning from the behavioral. They characterized denning as the physical act of reducing mobility and presumably conserving energy by entering a constructed or natural cavity, and hibernation as the physiological adaptations that allow bears to survive without food or water while in dens. Folk et al. (1976) and Hellgren (1998) considered ursids true hibernators and possibly the most highly refined example of this phenomenon.

Timing of den entry and emergence is an important facet of grizzly bear management in the Greater Yellowstone Ecosystem (GYE). Grizzly bears are sensitive to human disturbance at den sites, particularly if disturbances are correlated with the timing of den entry (Craighead and Craighead 1972). Mace and Waller (1997) speculated that the greatest potential for disturbance to grizzly bears by snowmobilers was during the spring when females with cubs of the year were still confined to the vicinity of dens or after bears had moved to gentler terrain more suitable to snowmobiling. Within the boundaries of Yellowstone National Park (YNP), motorized winter recreation is restricted to existing roads and occurs during winter months (late Dec–early Mar). Similar restrictions do not exist on National Forest lands surrounding YNP with the exception of designated wilderness, which prohibits motorized use. To minimize disturbance to bears, land managers making decisions regarding opening or closing of winter-use seasons require the best available information on chronology of denning events and patterns of spring movements.

The Interagency Grizzly Bear Study Team (IGBST) has been investigating life history aspects of grizzly bears in the GYE since 1975. Judd et al. (1986) previously described denning chronology using data collected during1975–80. Here we present a summary of denning chronology for different classes of grizzly bears in the GYE that includes data from 1975–99. We also present patterns of post-denning movements for different classes of bears.

STUDY AREA

Our study area (centered at 44.64°N, 110.52°W) contained approximately 37,500 km^2 in the states of Wyoming, Montana, and Idaho and encompassed YNP and portions of 6 National Forests that surround it. A major portion of the occupied grizzly bear habitat within the area is designated as the Yellowstone Grizzly Bear Recovery Zone (U.S. Fish and Wildlife Service 1993). The majority of grizzly bear denning activity was contained within the 23,850 km^2 recovery zone (Fig. 1).

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Fig. 1. Location of the Yellowstone Grizzly Bear Recovery Zone (shaded) in Idaho, Montana, and Wyoming, USA.

Geographically the GYE includes headwaters of the Missouri–Mississippi, Snake–Columbia, and Green–Colorado river systems, the Yellowstone Plateau, and 14 surrounding mountain ranges (Marston and Anderson 1991). Elevations in the recovery zone range from 1,307 to 3,809 m and average 2,450 m. Marston and Anderson (1991) suggested that notable changes between forested terrain of the mountains and rangelands of surrounding basins occur at 2,130 m. Cover types vary from alpine meadows above timberline, which occur at 2,900 m (Romme and Turner 1991), and whitebark pine (*Pinus albicaulis*) on high-elevation timbered slopes (2,600–2900 m), through subalpine fir (*Abies lasiocarpa*) on mid slopes (2,200–2,600 m), to lower elevation lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) cover types (1,900–2,200 m). Sage (*Artemisia tridentata*) dominated complexes are prevalent on mid-elevation plateaus and low elevation valley bottoms.

Mean maximum and minimum temperatures at Lake Ranger Station near the center of YNP are -5.3°C and -16.6°C during January and 21.7°C and 3.5°C during July (Temperature and Precipitation Station [TAPS], Yellowstone Lake, Wyoming, USA, 1948–99, unpublished data). Precipitation averages 51.3 cm annually, with 420.6 cm falling as snow, mostly in October–April. The frost-free period ranges from 60–90 days at lower elevations. In alpine zones, frost may occur at any time.

Important spring foods available to bears after den emergence include carrion from winter-killed ungulates, primarily elk (*Cervus elaphus*) and bison (*Bison bison*) (Green et al. 1997, Mattson 1997), elk calves, and cutthroat trout (*Oncorhynchus clarki*). Elk calves are obtained through predation during late May through early July (Gunther and Renkin 1990, Mattson 1997). Spawning cutthroat trout are also obtained through predation during mid May through July (Reinhart and Mattson 1990). Seeds from whitebark pine (Kendall 1983) and army cutworm moths (*Euxoa auxiliaris*; Mattson et al. 1991) are important late summer and fall foods. An inverse relationship between annual fall whitebark pine seed production and human-caused grizzly bear mortality has been demonstrated (Mattson et al. 1992).

Recent studies using ^{15}N and ^{13}C isotopes from hair samples from GYE grizzly bears suggests that meat may constitute as much as 79% and 45% of the annual diet for males and females, respectively (Jacoby et al. 1999). There is also evidence that suggests meat from ungulates becomes more important during years with poor whitebark pine cone crops (Mattson 1997).

METHODS

The IGBST has captured, radio-instrumented, and tracked grizzly bears in the GYE annually since 1975. We used culvert traps or Aldrich leg-hold snares to capture bears. All grizzly bears except dependent offspring (cubs or yearlings) captured during research trapping efforts were radio-instrumented. Adult bears were usually instrumented with radiocollars (Telonics, Mesa, Arizona, USA) with breakaway cotton inserts. Independent subadult bears were instrumented with expandable collars or glue-on hair transmitters. Blanchard (1985) described methods used to capture and radiomark bears. Aerial methods used to determine den entry and emergence of radiotagged bears were described by Judd et al. (1986). Since 1986, the primary objective for monitoring grizzly bears by the IGBST has been to estimate survivorship and fecundity. Because of this, frequency of radiomonitoring flights was reduced by half during late fall (10 vs. 5 days), winter, and early spring (14 vs. 7 days) from that described by Judd et al. (1986). Nevertheless, the addition of 2 decades of data substantially increased sample sizes over those used by Judd et al. (1986) to describe denning chronology of grizzly bears in the GYE.

Timing of den entry and emergence was estimated using methods similar to those described by Schwartz et al. (1987) and Mace and Waller (1997). Unlike those studies, however, we re-coded estimated Julian dates of denning events into week of occurrence, and we excluded data when differences between Julian date of last pre-den location (PD) and first Julian date located in den (FID) were >14 days. Estimated week of den entry was defined as (FID – PD)/2 + PD. We estimated the earliest and latest week of den entry by PD + 1 and FID – 1, respectively. Similarly, we estimated week of den emergence as (OD – LID)/2 + LID (OD = first Julian date out of den, LID = last in den), earliest week as (LID + 1), and latest week as (OD – 1). Estimates for duration of denning were determined only for bears that met the $\leq$14-day restriction for both their entry and emergence and followed methodology of Schwartz et al. (1987).

Results from 19 whitebark pine cone production transects (Blanchard 1990) read annually from 1980–99 were used to rate fall cone production. Years with a majority of trees producing cones below the overall median were considered poor. Years with a majority of trees above the overall median were considered good.

Climate data for 1975–99 were obtained from the Yellowstone Lake TAPS station. This station is located in the approximate center of grizzly bear distribution in the GYE and provided data representative of climatic influence on bears. Data included minimum, maximum, and mean daily temperatures, daily precipitation, and snow depth. These data were summarized to monthly minimum, maximum, and mean temperatures, mean monthly precipitation, and snow depth.

We investigated patterns of post emergence movements relative to den locations by calculating distances from each radiolocation to the den location for that bear, through 15 June only for bears with OD – LID $\leq$ 14 days. When investigating elevations at den sites, we used all locations for which we had an estimate of den emergence and did not restrict our sample. Estimates of elevation (m) at den sites and spring locations were derived from a 30-m Digital Elevation Model and classified using the program ArcView (version 3.2, Environmental Systems Research Institute, Redlands, California, USA). Average error for our aerial telemetry was 250 m (IGBST unpublished data). We assume that telemetry error was unbiased, and for our purpose here could be ignored.

We considered annual denning events independent, and determined that week of entry and emergence approximated normal distributions. We used Student's *t*-tests to investigate difference in week of denning chronology between male and females bears and between subadult and adult within the same sex. Throughout, we use the terms "cubs" for offspring in their first year of life, and "dependent offspring" to include cubs as well as older young still dependent on their mother. We used ANOVA to investigate differences in week of den events among 3 classes of bears. For differences in week of den entry, classes were: (1) known pregnant females, defined as females that were known to emerge with cubs the following spring; (2) other females, which included subadult females, solitary adult females that did not emerge with cubs the following spring, and females that entered dens with dependent young; and (3) males. For differences in week of emergence, classes were defined as: (1) females with cubs, (2) other females, and (3) males. Sample sizes were not sufficient to designate additional classes for either entry or emergence. When significant ($P < 0.05$) ANOVA results occurred, we used Tukey's HSD (honestly significant difference) *post hoc* procedure ($P < 0.10$) to identify where those differences occurred among classes. Student's *t*-tests were used to investigate differences in week of den entry between years exhibiting good verses poor whitebark pine cone production within each class of bears. We used Pearson's correlation coefficient to quantify relationships among the different methods for estimating week of entry and emergence, between weeks of den entry and emergence and time (i.e., 1975–99) within classes of bears, and between various monthly climate statistics and time. Statistical comparisons were completed using SPSS (version 10.0.7, SPSS Inc., Chicago, Illinois, USA).

RESULTS

Den Entry

We obtained 123 estimates of week denned (female n = 76, male n = 47), which came from 49 individual females ($\bar{x}$ =1.5/bear, range 1–6), and 40 individual males ($\bar{x}$ = 1.2/bear, range 1–2). Females differed from males for mean estimated week, mean earliest week, and mean latest week of den entry. Among female bears, mean entry was the first week in November and ranged from the fourth week in September to third week in December. Mean week of den entry for males was the second week in November and ranged from second week in October to second week in December. No differences in mean estimated week, mean earliest week, or mean latest week of entry were evident between subadult (ages <5) and adult classes ($P > 0.25$) within sexes. Known pregnant females, other females, and male bears differed for week of den entry using all 3 measures (Table 1). Tukey's HSD results varied somewhat depending on the measure used but consistently indicated that known pregnant females entered dens earlier than males and earlier than other females when mean earliest week was used (Table 1). All 3 methods (i.e., estimated week, earliest week, and latest week) were highly correlated (Pearson's $r > 0.95$) and provided similar results. We used only estimated week denned to show cumulative percent of entry by week for the 3 classes of bears (Fig. 2).

During 1980–99 we classified annual whitebark pine cone production as poor (n = 7) and good (n = 13) years. We detected no differences ($P > 0.5$) in estimated week of den entry between good and poor years within any class of bears (sex, age, and reproductive status).

Table 1. Mean week of den entry and emergence among 3 classes of grizzly bears in the Greater Yellowstone Ecosystem, 1975–99, using 3 methods of estimation. Common letter after date indicates no difference among classes using Tukey's honestly significant differences (HSD) at $P < 0.10$.

Den event	Class	*n*	Earliest week	Estimated week	Latest week
Entry	Known pregnant females	31	4th week Oct [a]	1st week Nov [a]	1st week Nov [a]
	Other females	45	1st week Nov [b]	2nd week Nov [ab]	2nd week Nov [ab]
	Males	47	2nd week Nov [b]	2nd week Nov [b]	3rd week Nov [b]
	ANOVA *P*		0.011	0.015	0.013
Emergence	Females with cubs	35	3rd week Apr [a]	4th week Apr [a]	4th week Apr [a]
	Other females	51	3rd week Apr [a]	3rd week Apr [a]	3rd week Apr [a]
	Males	29	3rd week Mar [b]	4th week Mar [b]	4th week Mar [b]
	ANOVA *P*		<0.0001	<0.0001	<0.0001

We noted a temporal trend only among adult male bears ($n = 32$); estimated week of den entry was significantly correlated with year ($r = 0.58$, $P < 0.001$, i.e., male bears denned later during more recent years). Among the fall (Sep–Dec) weather parameters investigated, November minimum monthly temperatures were positively correlated with year ($r = 0.54$, $P = 0.005$) during 1975–99. Other weather parameters were uncorrelated with year.

Den Emergence

We obtained 115 estimates for week of den emergence (female $n = 86$, male $n = 29$), which came from 52 individual females ($\bar{x} = 1.7$/bear, range 1–5), and 21 individual males($\bar{x} = 1.4$/bear, range 1–3). Males and females differed using all 3 measures of emergence. Mean week of den emergence among female bears was the third week of April and ranged from the third week in March to the fourth week in May. Among males, mean emergence was the fourth week in March and ranged from first week in February to the fourth week in May. We found no difference in timing of emergence ($P > 0.10$) between subadult and adult classes of either sex. Female classes differed from males in mean week of emergence (Table 1). However, our data provided no grounds for accepting that a true difference existed between females with cubs and other females in den emergence (Fig. 3).

Only among other females was week of den emergence significantly correlated with year ($r = 0.623$, $P < 0.001$), i.e., these females emerged from dens later during more recent years. However, no significant correlation between spring (Mar–May) weather parameters and years was evident.

Denning Duration

We obtained length of denning period for 44 events that had credible entry and emergence weeks (Table 2). Durations were obtained for 32 female ($\bar{x} = 1.7$/bear, range 1–5) and 12 male ($\bar{x} = 1.1$/bear, range 1–2) bears. Females that emerged from dens with cubs typically denned longer than other classes, averaging 171 days. Males denned for the shortest period, averaging 131 days. Differences in den duration between females that emerged with cubs and other classes of bears were typically due to earlier entry of pregnant females.

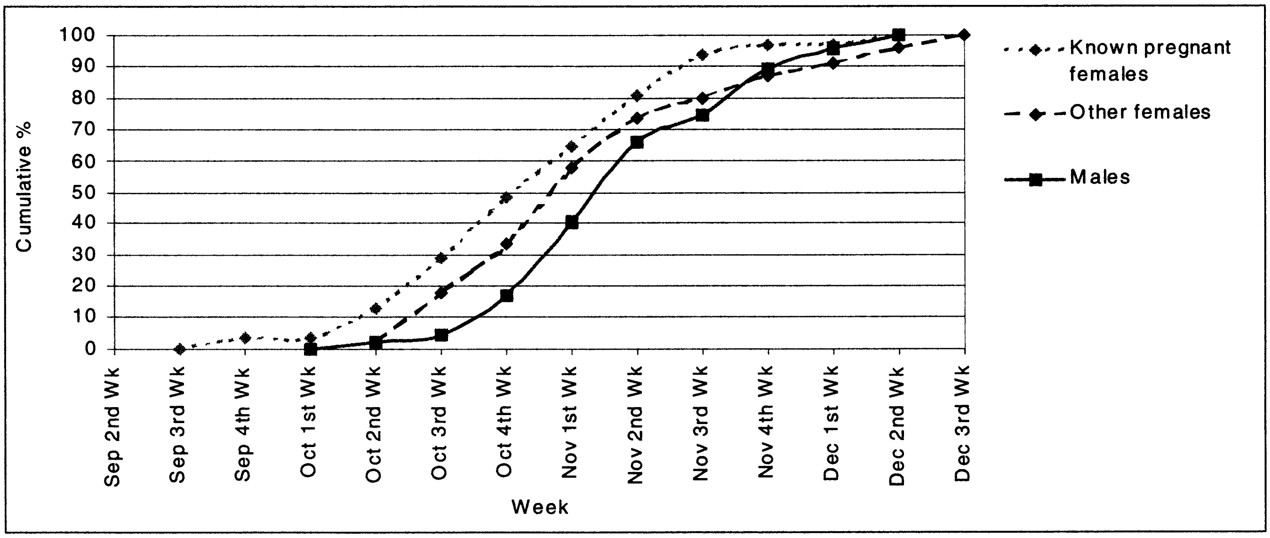

Fig. 2. Cumulative percent of grizzly bears denned by week in the Greater Yellowstone Ecosystem, 1975–99. Week of den entry was determined for bears if the days between their last known pre-den location and their first known date denned was ≤14 days.

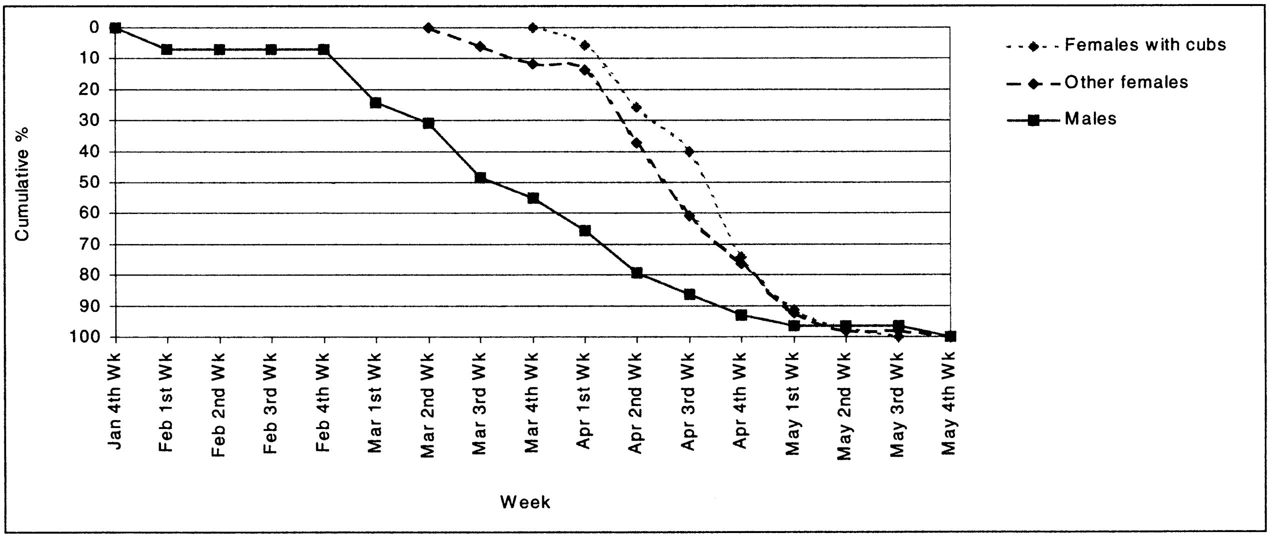

Fig. 3. Cumulative percent of bears emerged from dens by week in the Greater Yellowstone Ecosystem, 1975–99. Week of den emergence was determined for bears if the days between their last known location in dens and their first known active location was ≤14 days.

Table 2. Mean den duration among 3 classes of grizzly bears in the Greater Yellowstone Ecosystem, 1975–99, using 3 methods of estimation. Common letter after entry indicates no difference among classes using Tukey's honestly significant differences (HSD) at *P* < 0.10.

Class	*n*	Days	Minimum days	Maximum days
Females with cubs	18	171*a*	166*a*	177*a*
Other females	14	151*b*	147*b*	156*b*
Males	12	131*c*	125*c*	137*c*
ANOVA *P*		<0.0001	<0.0001	<0.0001

Elevation at Den Sites

We rejected the null hypothesis that all 3 classes of bears denned at the same distribution of elevations ($F = 3.83$, 2 df, $P = 0.023$). Known pregnant females denned higher (HSD, $P < 0.035$) than other females or male bears. Mean elevation at den sites for females that emerged from dens with cubs was 2,696 m ($n = 49$, SD = 271). We observed no difference in elevation at den sites between other females and male bears. Mean elevation at den sites for other females and males were 2,581 m ($n = 102$, SD = 278) and 2,574 m ($n = 83$, SD = 248), respectively.

Post Emergence Movements and Elevation

Females with cubs typically restricted their movements to within 3 km of den sites until late May (Fig. 4). Females with cubs also remained at higher elevations relative to other classes of bears until late May (Fig. 5). Other female bears not accompanied by cubs moved to lower, presumably snow-free elevations soon after emerging from dens. Mean elevations used by all classes of bear converged in late May.

DISCUSSION

The chronology of denning for grizzly bears in the GYE was qualitatively similar to that reported by Judd et al. (1986), even though number of estimated entry and emergence dates used in this analysis increased by 76% and 109%, respectively, and the frequency of spring and fall telemetry flights was reduced during recent years. Our similar results with reduced effort suggest that long-term monitoring at a lower intensity may be sufficient for determining denning chronology. The reduced flight frequency required us to impose the ≤14-day restriction to increase accuracy, but may also have affected our estimates for male entry and emergence. Males entered dens later and emerged earlier than other classes of bears, coinciding with our reduced flight frequency. If a bear was not located during this period, it was omitted because of the ≤14 day limit, thereby biasing results because early emerging or late denning individuals were excluded. For example, we knew of one male that was still active during the third week in December but not located again until late January. This resulted in his exclusion from our analysis although his late denning behavior may have had biological importance for managers. Notably, this same relationship also allowed us to collect considerably more data on reproducing females because they were denning and emerging when flights were most frequent. This was desirable because these bears are likely the most sensitive to disturbance, requiring the best possible denning data for sound management.

Timing of den entry is probably influenced by food availability and weather (Craighead and Craighead 1972, Van Daele et al. 1990). We investigated whether timing of den entry was correlated with whitebark pine cone pro-

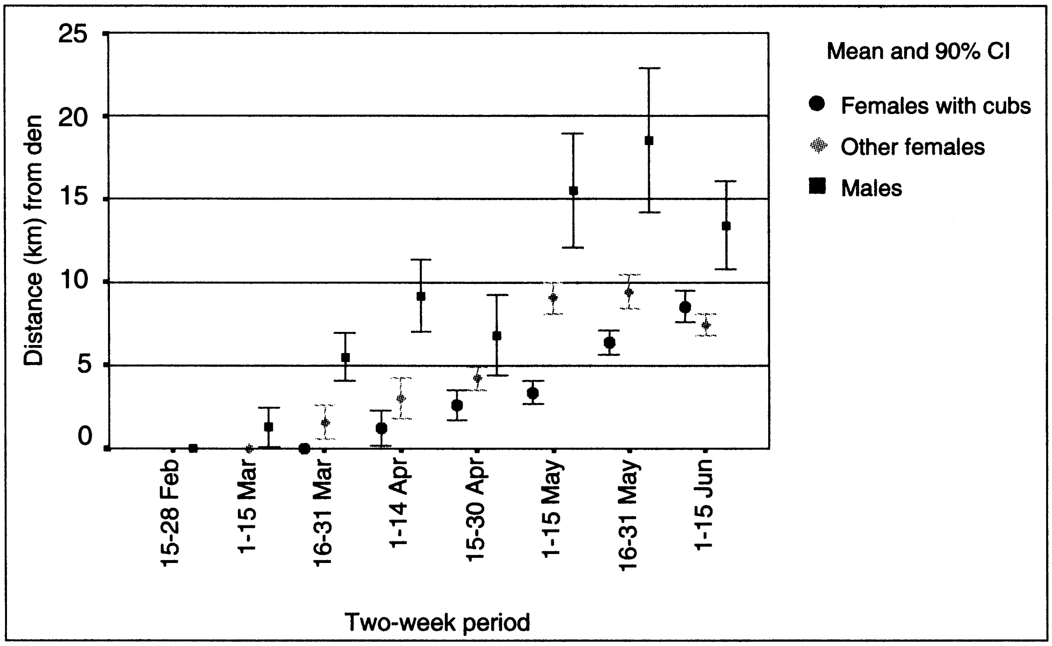

Fig. 4. Mean distance (km) from dens for females with cubs, other females, and male bears by 2-week period for grizzly bears in the Greater Yellowstone Ecosystem, 1975–99.

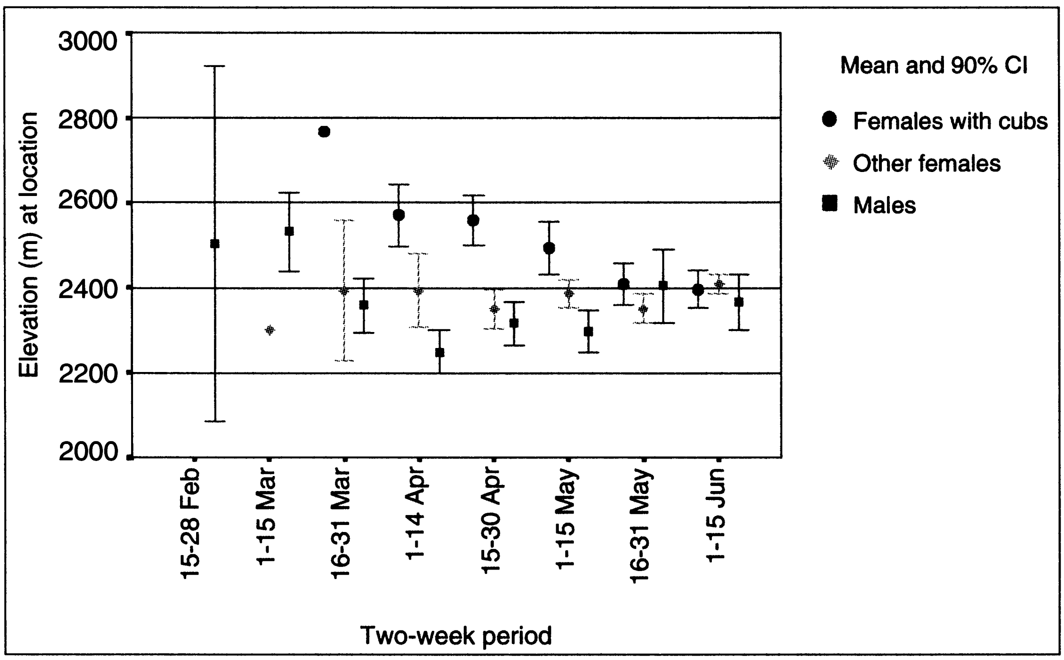

Fig. 5. Mean elevation (m) of spring locations for females with cubs, other females, and male bears by 2-week period for grizzly bears in the Greater Yellowstone Ecosystem, 1975–99.

duction during 1980–99 and found no significant effect. However, we do not conclude from this that such a relationship does not exist, only that we were unable to detect it using our single index of fall food abundance. Although the GYE does not contain substantial amounts of alternative fall mast crops, other foods undoubtedly become more important during years exhibiting poor cone production. Mattson (1997) suggested that meat from ungulates became more important during years with poor cone production.

We did not investigate the influence of specific annual weather events on the timing of den entry because reduced flight frequency prevented us from accurately correlating weather events with entry. We observed a trend toward later den entry among adult males in recent years and a corresponding trend of increasing minimum temperatures during November over the period 1975–99. Although these observations do not represent cause and effect, it is interesting that among all sex, age, and reproductive classes, adult males are most likely to remain active if foods are available and weather conditions permit (Van Daele et al. 1990).

Females with cubs for which we had data on timing of den emergence denned at higher elevations and tended to remain at higher elevations for several weeks following emergence, unlike the other classes of bears. Using a larger sample of den locations that was not restricted by knowledge of timing of emergence, Podruzny et al. (2002) documented no significant difference in elevation at den sites among classes of bears in the GYE. Our results were influenced by 2 extreme values from 1 individual. If we excluded these values, no statistically significant difference in elevation at den sites was evident, although the mean elevation for den sites of known pregnant females was still approximately 100 m higher than other classes of bears. Whether this trend is biologically significant to grizzly bears in the GYE is debatable. It does point to possible spatial separation between females that emerge from dens with vulnerable cubs and other classes of bears.

Linnell et al. (2000) compiled a comprehensive summary of denning chronology for brown bear populations worldwide. They reported variations in denning behavior in all North American brown bear populations, but all bears entered dens each winter except on Kodiak Island, Alaska, where 25% of radiocollared males remained active during at least 1 winter of study (Van Daele et al. 1990). These Kodiak males spent much of their time bedded, intermittently traveling short distances, and appeared to be in a state of "walking hibernation" (Nelson et al. 1983).

Latitude also appears to influence denning, with bears in northern latitudes denning earlier and longer than bears in southern latitudes (Fig. 6). Nevertheless, generalizations are apparent across all latitudes and environmental conditions, such as the tendency for pregnant females to den first and for longer periods than adult males (Linnell et al. 2000). Our results corroborate these generalizations. Denning dates reported here are consistent with latitudinal trends (Fig. 6). Pregnant females also were the first class to den, typically 1–2 weeks before all other classes, and males were the last group to enter, spending 20–40 days less in dens than other bears.

The chronology of denning events we reported should be useful in land management decisions aimed at adjusting timing of human activities to minimize disturbances. Security at den sites appears to be important, especially around the time of entry. Craighead and Craighead (1972) reported that bears abandoned dens less frequently if disturbed late in the winter than close to time of entry. Increases in activity and heart rate of denning bears, and 1

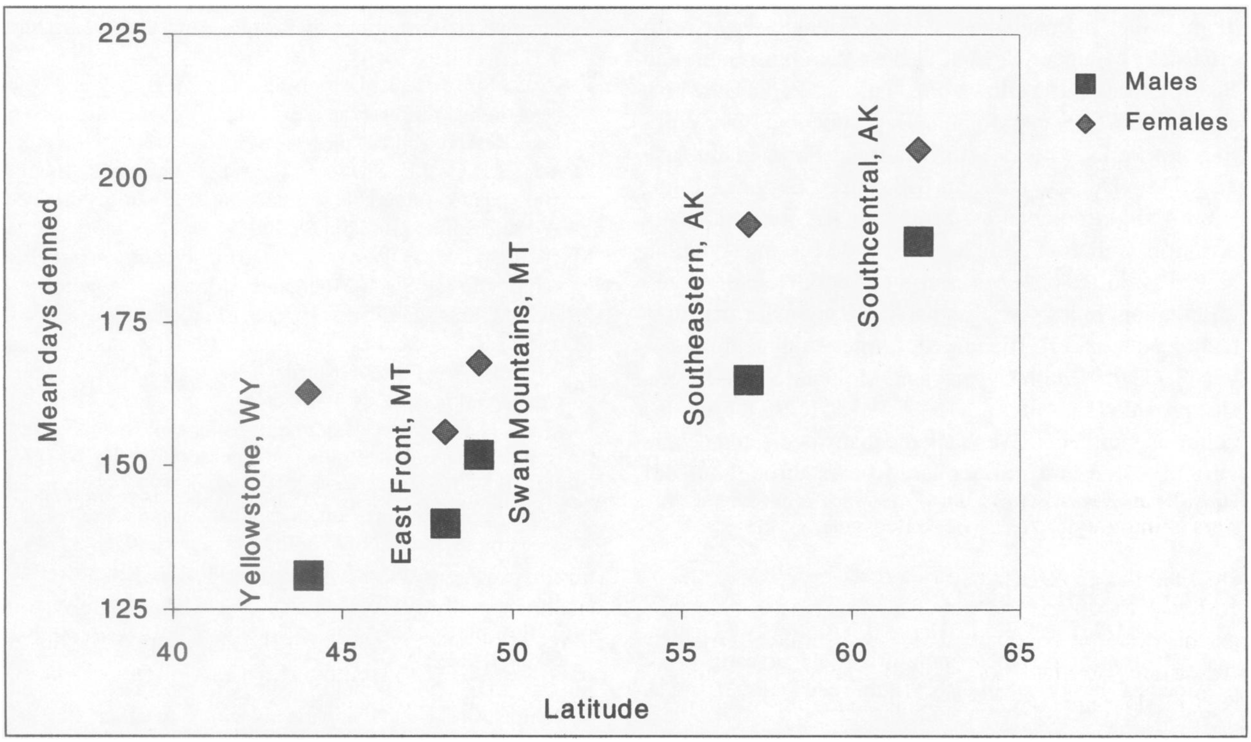

Fig. 6. Relationship between latitude and mean number of days denned for male and female grizzly bears from 5 North American populations (Aune et al. 1986, Schoen et al. 1987, Miller 1990, Mace and Waller 1997, this study).

instance of possible den abandonment due to seismic crews working near den sites, have been reported (Reynolds et al. 1986), even though that activity was considered minimal. The physiological and demographic impacts of these types of disturbances are not well understood.

Potential for negative impacts due to disturbance of emerging females with newborn cubs may be more critical. Because of their limited mobility early in the spring, cubs may be susceptible to abandonment by females when disturbed. Mace and Waller (1997) believed the greatest potential for impact to bears was during the spring when females with cubs were still near their dens or shortly afterward when they moved to gentler terrain where potentially disruptive snowmobiling was more common. Females with cubs tend to remain near their dens for up to several weeks following emergence (Craighead and Craighead 1972, Vroom et al. 1980, this study), and thus may be vulnerable to disturbance.

Combining our observations on denning chronology with descriptions of suitable denning habitats for grizzly bears in the GYE (Podruzny et al. 2002) should provide managers with information necessary to limit disturbances to denning grizzly bears in the GYE.

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