

THE EFFECTS OF DEVELOPMENTS AND PRIMARY ROADS ON GRIZZLY BEAR HABITAT USE IN YELLOWSTONE NATIONAL PARK, WYOMING

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Abstract: Aerial locations of radio-instrumented grizzly bears (*Ursus arctos*) were used to analyze effects of human activity associated with developments and primary roads on grizzly bear habitat use in Yellowstone National Park. Grizzly bear occupancy of habitat near human facilities was reduced, efficient foraging strategies were disrupted, and cohorts tending to be subordinate or security-conscious were displaced into habitat nearer developments by more dominant cohorts, particularly during summer and fall. Adult females and subadult males residing closer to developments were management-trapped at a higher rate than animals of the same class residing farther away. Adult females and subadults bore a disproportionate part of costs associated with avoiding roads and developments. For this reason and because adult females are generally thought to operate under considerable energetic duress in the Yellowstone area, avoidance of developments and roads may have resulted in higher mortality and lower productivity among the adult female cohort.

Int. Conf. Bear Res. and Manage. 7:259–273

Grizzly bear populations have typically been reduced or eliminated after sustained contact with Western civilizations. This has primarily been a result of human-caused mortalities; habitat loss has been a secondary factor (Storer and Trevis 1955, Brown 1985). Therefore, management and research have been concerned with defining how much mortality and habitat loss a bear population can tolerate and remain viable. Key questions have been (1) how do bears respond to humans, and (2) how does a given response influence risk for, and habitat use by, grizzly bears?

The consequences of bear-human encounters to humans have been described and analyzed (e.g., Herrero 1976, Merrill 1978, Chester 1980, Herrero 1985, Jope 1985). Other research has attempted to determine encounter effects on bears as a function of individual bear history, site, and season (Schleyer et al. 1984, Haroldson and Mattson 1985). Still other studies have investigated more general impacts of human activities, primarily in association with logging and hydrocarbon exploration and development (Elgmork 1978, Harding and Nagy 1980, Schallenberger 1980, Zager 1980, Aune et al. 1984, McLellan and Mace 1985).

The effect of human activities on bears is an important issue in Yellowstone National Park; most human activities are concentrated at roads and developments. More than 2 million people visit the park each year during the period that grizzly bears are active. Fifty percent of the park is within 8 km of a primary road and within 11.5 km of a village or front-country campground. Furthermore, the Yellowstone grizzly bear population appears to be marginally viable (Knight and Eberhardt 1984, 1985). Therefore, the Interagency Grizzly Bear Study Team (IGBST)

used existing data to analyze the effects of roads and human developments on grizzly bear habitat use in Yellowstone Park.

Our objectives were to (1) determine if observed levels of bear use were equal to that expected along roads and around developments; (2) determine if productivity of habitat occupied by bears was equal to that expected with nonselective use along roads and around developments; (3) quantify any evident avoidance by bears of roads and developments and; (4) determine if representation of different sex and age bear classes differed between areas close to and more remote from human facilities.

STUDY AREA

Yellowstone National Park (Fig. 1) comprised the analysis area. Most elevations in the park are from 2,100 to 2,450 m. Topography is dominated by an extensive central plateau and encircling higher relief mountains. Bedrock in many areas is of recent volcanic origin. Other areas are underlain by older volcanic and uplifted sedimentary strata (Keefer 1976).

The analysis area lies principally in the subalpine zone. Closed-canopy forest covered approximately 75% of the area. Most of this forest consisted of lodgepole pine (*Pinus contorta*) dominated stands in sapling to over-mature stages. Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) dominated stands were more common on high-relief topography underlain by andesitic bedrock. Extensive nonforest areas occurred primarily below 2,125 m and generally reflected warmer, drier conditions. Further details of the study area are available in Knight and Eberhardt (1985).

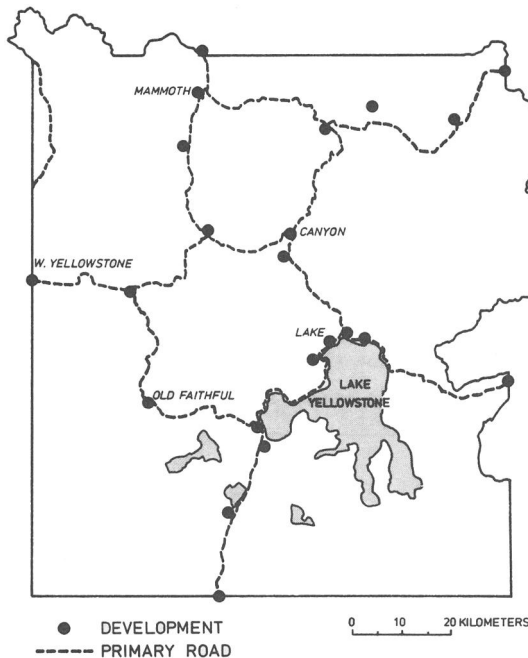


Fig. 1. Yellowstone National Park analysis area primary roads and developments.

METHODS

Between 1974 and 1983, 2,561 aerial locations of radio-instrumented grizzly bears were made by the IGBST within Yellowstone National Park (Knight et al. 1984). By 1983 computer files of digitized habitat type (Mueggler and Stewart 1980, Steele et al. 1983) and cover type (Despain 1986) maps were available for Yellowstone Park; methodology had also been developed for deriving grizzly bear-specific coefficients of habitat productivity for habitat and cover types (Mattson et al. 1986). These coefficients or habitat productivity scores were derived from analysis of grizzly bear scats and feedsite data. Values ranged from 0.0 to 1.0 and varied by season. We used these data and methodology, a 1.5-km interval grid map, and digitized road and development data for our analysis.

We analyzed 2 different-sized areas that bordered and were parallel to roads and concentric to developments. The smaller area was 1,500 m wide and was included in the larger 15-km-wide area. These 2 different-sized analysis areas were subdivided into 15 zones paralleling roads or concentric to developments; each zone was 100 m wide in the 1,500-m area and 1 km wide in the 15-km area. Thus the

1,500-m analysis area was included within the 1st 2 zones of the 15-km analysis area. An additional 16th zone was created for the 2 different-sized analysis areas by dividing the zone nearest to and bordering a road or development in half, creating 2 50-m-wide zones in the 1,500-m-wide analysis area and 2 500-m-wide zones in the 15-km-wide analysis area. Bear locations and grid points were allocated to zones of the 1,500-m and 15-km analysis areas based on distance to the nearest road or development. Zones were thereby the basis for chi-square analysis and graphics display of the data. We expected the 1,500-m analysis to be sensitive to habitat use by individual bears residing near roads and developments; we expected the 15-km analysis to be sensitive to population adjustments such as possible avoidance of human facilities by wary bears.

We selected zone widths of 100 m and 1 km to provide sensitivity to any effects of geographic extent and degree associated with human facilities. If more than 4 zones ($> 20\%$ of total zones) contained fewer than 5 bear locations, the zone widths for the entire analysis area were changed and data further pooled (Sokal and Rolf 1969). Thus 1,500-m analysis area zones used in statistical analysis were in some cases 200 and 300 m rather than 100 m wide. In the end, zone widths used for analysis reflected desired sensitivity and limitations of our data.

Habitat productivity scores were calculated for bear locations and point intersections of the 1.5-km interval grid. Scores were derived from intersecting 0.5-km radius scan areas, for which bear locations and grid points served as foci, and digital map data. Scan area scores were habitat type productivity scores weighted by the proportion of the area represented by the habitat type.

Chi-square was used to test the hypothesis that observed frequency of bear locations across zones corresponded to that expected. Our expected frequency in each zone was proportionate to zone area weighted by mean zone habitat productivity score; mean zone habitat productivity score was calculated from scores associated with grid points included within the zone. We considered $P < 0.10$ to be significant. The analysis was stratified by season and by reference to primary road or development. Seasons were defined as spring (1 Mar–31 May), summer (1 Jun–31 Aug), and fall (1 Sep–15 Nov).

Boundaries for chi-square analysis were established by an iterative process. Observed and expected frequencies were initially examined across all zones. Ma-

major sign-consistent deviations of observed from expected use were noted progressively outward from either roads or developments. The 1st sign break in a major pattern (i.e., observed intersecting expected) was designated as midpoint of the larger area for which we conducted chi-square analysis. We considered mean sign-consistent deviation of observed from expected use greater than 12% over 3 or more sequential zones to constitute a major pattern. In the absence of major patterns, all 16 zones were included for analysis. This procedure was followed so as to exclude areas outside any pattern that could be attributed to effects of front-country facilities.

Graphic display of data for the 1st 2 zones (out to 1 km) of the 15-km analysis area did not necessarily correspond to broad patterns evident by plotting data for all zones of the 1,500-m analysis area; observed vs. expected levels of use often differed within 1,000 m of roads and developments when comparing the 15-km and 1,500 m analyses. This resulted from rescaling expected proportions for the 1,000-m area when a larger area was considered in the 15-km analysis. Observed use could have been less than expected within 500 m of a road on the 1,500-m scale, but if overall bear use was much higher than expected within 2 km of roads on the 15-km scale, then the 1,500-m analysis result would not have been duplicated by the 15-km analysis. This is 1 reason why 2 different size analysis areas were used.

Mean number of management-trappings per year was calculated for 26 bears whose locations were analyzed. We used the number of years a bear was known to be alive, 1975 through 1983, in the denominator. We did not use bears with fewer than 5 years record. There was a high variance among trappings per year because mean per-year trapping rates were low (0.17 trappings/year) and virtually all trappings occurred during extremely poor food years—at 4–5 year intervals (Mattson 1987). Only adult females and subadult males were used because mortality and trapping of these cohorts are much more strongly related to year-to-year fluctuations in habitat productivity than any other cohort (Mattson 1987). After accounting for effects attributable to interval between poor food years and among class vulnerability to trapping, our sample size was reduced to 13 bears, of which 3 ranged closer to, and 10 farther from developments.

We use “wary” to denote bears inclined to avoid humans and their facilities; such tendencies have been noted for individual bears by Haroldson and Mattson

(1985) and Gunther and Renkin (1985). We use “habituated” to denote bears less inclined to avoid humans, and apparently tolerant of close proximity human presence (Herrero 1985). “Food conditioned” bears were habituated bears that characteristically associated feeding opportunities with human facilities (Herrero 1985). We used 2 terms to characterize habitat: “habitat productivity” related to density and value of foods; “usable habitat” related to effective resource availability given actions taken by bears to avoid humans and other bears.

We used regression and correlation analysis to test relationships among cohort zone representation and between cohort representation and zone habitat productivity scores. Multiple regression analysis was used to elucidate more complex hypothesized relationships. Transformed and untransformed data were used. We hypothesized nonlinear relationships between cohort representation and habitat productivity. The bases for specific regressions and correlations were hypotheses arising from previous work within and outside the Yellowstone area; we did not test or accept relationships not suggested or supported by previous research.

RESULTS

Habitat Productivity Scores and Nonforest Area

Zone habitat productivity scores varied with distance from roads and developments, and with season (Fig. 2). Spring scores were highest within 5–6 km and peaked within the 1st kilometer of roads and developments. Summer and fall scores were highest generally beyond 8 km. Fall scores peaked between 10 and 12 km and were comparatively low within 6 km.

Percent nonforest area peaked adjacent to roads and developments, and was much lower beyond 2–3 km (Fig. 3). This distribution is because many facilities are located in valleys at lower elevations, where warmer and drier conditions resulted in more nonforest habitat.

1,500 m Chi-square Analysis

Observed bear zone use within 1,500 m of roads differed from expected to a greater extent than within 1,500 m of developments (Figs. 4 and 5). Bear zone use differed significantly from that expected along roads during spring and summer, but not during fall. Less use than expected was evident out to 500 m of

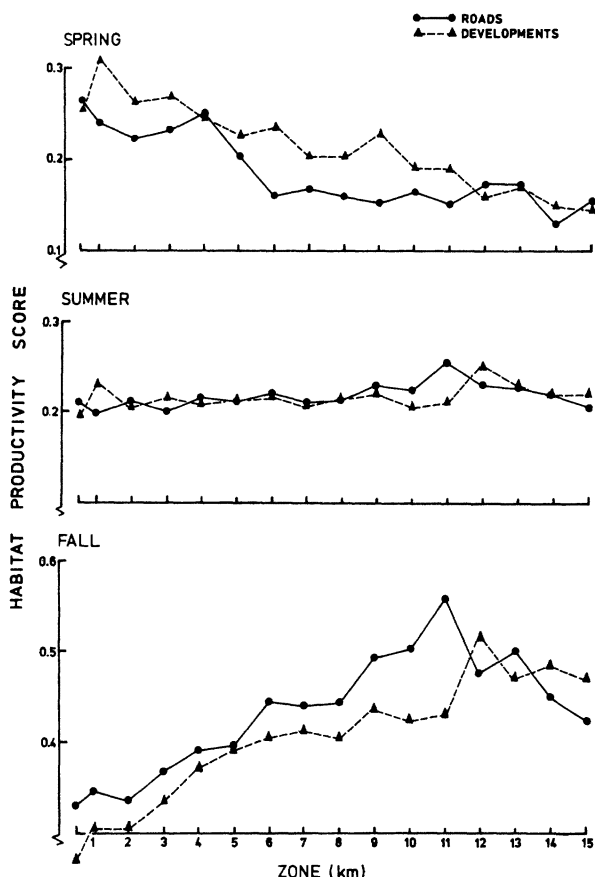


Fig. 2. Average grid-point scan area habitat productivity scores for road and development 15-km analysis zones, by season; zone numbers correspond to outer zone boundary in km from road or development.

roads during spring. Summer bear locations along roads showed a similar pattern but differed by use nearly equal to that expected between 50 and 200 m.

Zone bear use differed significantly from that expected within 1,500 m of developments only during fall when use tended to be greater than expected closer to developments. Summer levels of bear use corresponded closely to that expected. Spring analysis was precluded by insufficient data.

15 km Chi-square Analysis

Observed bear use within 15 km of roads differed significantly from expected during all seasons and within 15 km of developments during summer and fall (Figs. 6 and 7). Except within 500 m, bear use was substantially greater than expected within 2 km of roads during spring; between 2 and 5 km, bear use was substantially less than expected. During summer,

observed use was substantially less than expected within 500 m and between 7 and 9 km of roads. During fall observed use was less than expected out to 4 km and between 7 and 8 km. Less than expected use within 500 m of roads during spring and summer agrees with results of the 1,500-m analysis.

A double pattern of observed use greater than and less than expected was evident around developments particularly during summer. Observed use approximated expected use within 2 km of developments in summer and within 1 km of developments in fall. Observed use was less than expected between 2 and 5 km and 7 and 9 km during summer and between 1 and 4 km and beyond 7 km during fall. Generally, results of the 15-km analysis for the 1-km adjoining developments supported results of the 1,500-m analysis.

Habitat Selection

In nearly all zones beyond the apparent influence of roads and developments, grizzly bears occupied habitat substantially more productive than the average for the zone (Figs. 8 and 9). In all zones closer to roads and developments, except along roads during spring, productivity of habitat occupied by bears was nearly equal to or even less than the zone average. This tendency for bears to occupy less productive habitat extended out to 3 km around developments during spring and summer, 2 km along roads during summer, and 4 km along roads during fall. A similar though less consistent pattern was evident out to 3

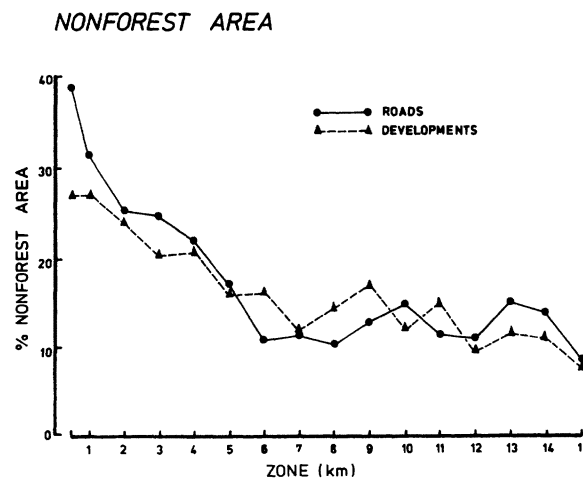


Fig. 3. Percent nonforest area for road and development 15-km analysis zones; zone numbers correspond to outer zone boundary in km from road or development.

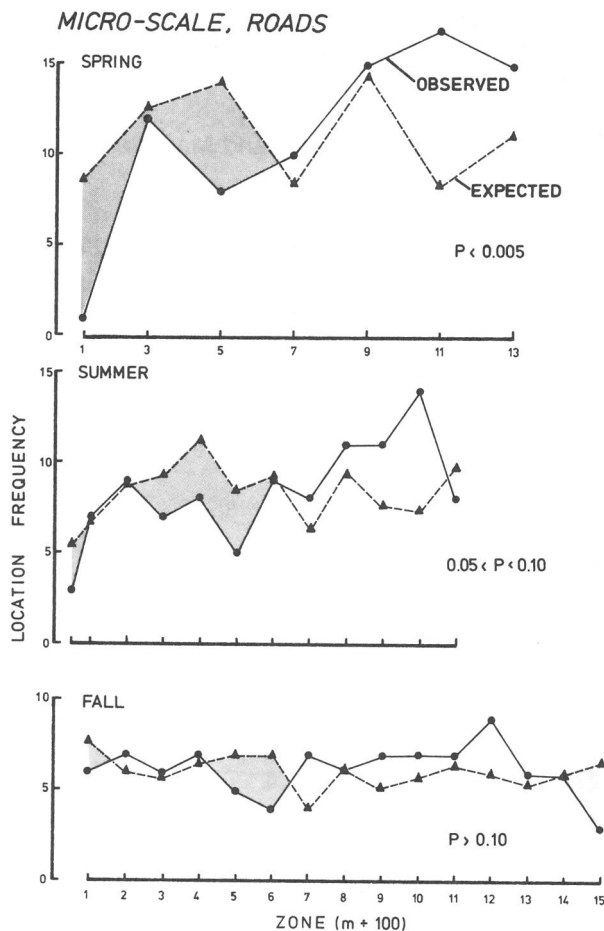


Fig. 4. Observed (bear location) and expected (weighted grid-point) frequencies for 1,500-m analysis zones, by season, with respect to roads. Chi-square analysis P values are given.

km around developments during fall. Population locations for bear location and grid point habitat productivity scores differed significantly beyond (Mann-Whitney U test; $P = 0.000$, $P = 0.000$, $P = 0.000$ for spring, summer, and fall, respectively) but not within 3 km of developments ($P = 0.480$, $P = 0.893$, $P = 0.197$, respectively) during all seasons. Along roads, population locations differed significantly beyond 2 km during spring and summer and 4 km during fall ($P = 0.000$, $P = 0.000$, $P = 0.000$, respectively); population locations differed significantly within 2 km of roads during spring ($P = 0.000$), but not within 2 km and 4 km of roads during summer and fall ($P = 0.423$, $P = 0.233$, respectively). Sample sizes and average habitat productivity scores for grid point and bear location scan areas for each zone and season are given in Table 1.

Distribution of Bear Cohorts

Different cohorts of bears were not equally represented across 15-km analysis zones around developments (Table 2). Considerable among-zone variation was evident for subadult females during summer, subadult males during fall, and all cohorts except females during spring. Low variation characterized adult females during spring and summer, and subadult females during fall.

Some spring and summer bear cohort zone distributions were related to habitat productivity and distribution of other bear cohorts. Spring adult female zone proportions were positively exponentially related to spring habitat productivity scores (Fig. 10); fall adult male proportions were positively related to fall scores (Fig. 11). Adult female and subadult male fall location proportions were 1st negatively related to adult male proportions and, 2nd, positively related to fall productivity scores; after accounting for distribution of adult males, adult females and subadult males were proportionately distributed with respect to habitat productivity. Adult females and subadult

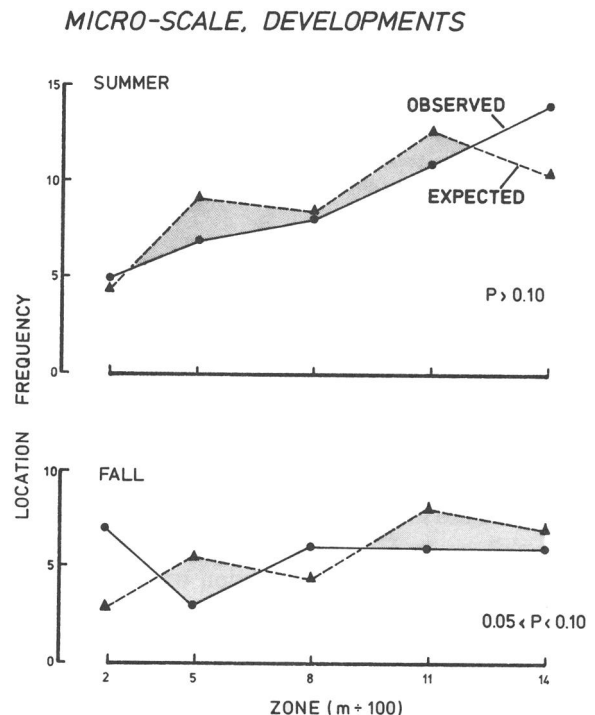


Fig. 5. Observed (bear location) and expected (weighted grid-point) frequencies for 1,500-m analysis zones, by season, with respect to developments. Chi-square analysis P values are given.

MACRO-SCALE, DEVELOPMENTS

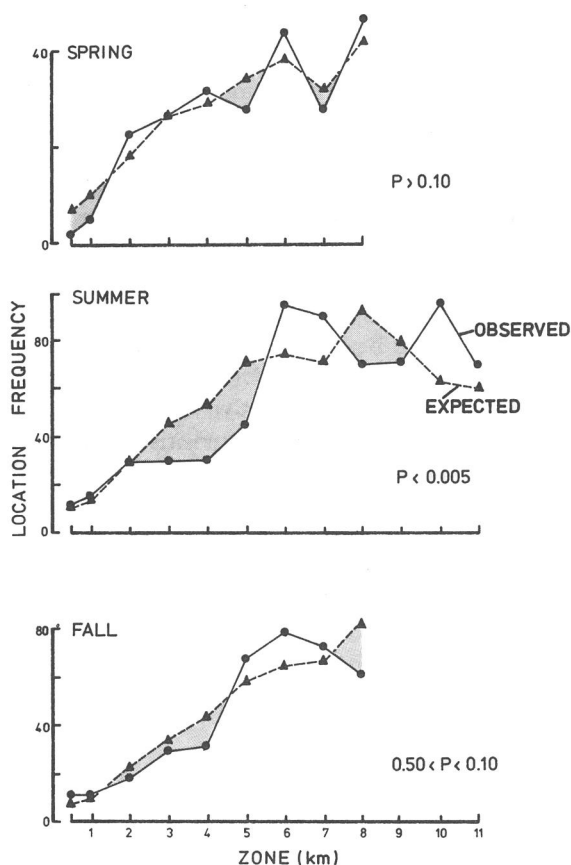


Fig. 6. Observed (bear location) and expected (weighted grid-point) frequencies for 15-km analysis zones, by season, with respect to developments. Chi-square analysis P values are given.

males were considered together during fall because of similar vulnerabilities; mortality in these cohorts was apparently responsive to habitat conditions (Mattson 1987); and virtually all known mortality in these cohorts has been caused by humans (Knight et al. 1987).

During summer, bear cohort zone distributions were related to that of other bear cohorts and distance to developments. Distribution of subadults was negatively correlated with distribution of adult females ($r = -0.91$, $P = 0.002$). Zone distribution of females with cubs-of-the-year was negatively related to distribution of other adult female classes (OADF) (lone and with yearlings or 2-year-olds). Females with cubs-of-the-year were also the only cohort whose distribution was positively related to distance from developments (DIST) without also being positively

related to habitat productivity: $y = -0.112 - 0.198 \ln \text{OADF} + 0.715 \times 10^{-3} \text{DIST}^3$; $r^2 = 0.76$, $P = 0.028$.

Individual Bear Distributions and Management Histories

Bears were concentrated in zones where use was greater than expected during summer around developments. In zones where observed bear use was near equal to or greater than expected (0–2 km, 5–7 km, 9–11 km), 3, 7, and 12 bears, respectively, had peak location densities. In intervening zones where bear use was less than expected (2–5 km, 7–9 km), 2 and 2 bears, respectively, had peak location densities.

MACRO-SCALE, ROADS

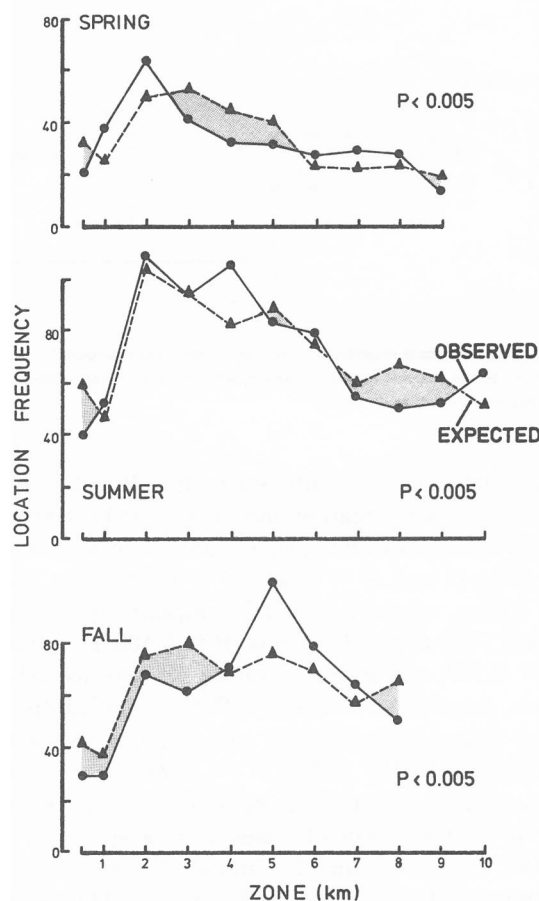


Fig. 7. Observed (bear location) and expected (weighted grid-point) frequencies for 15-km analysis zones, by season, with respect to roads. Chi-square analysis P values are given.

DEVELOPMENTS

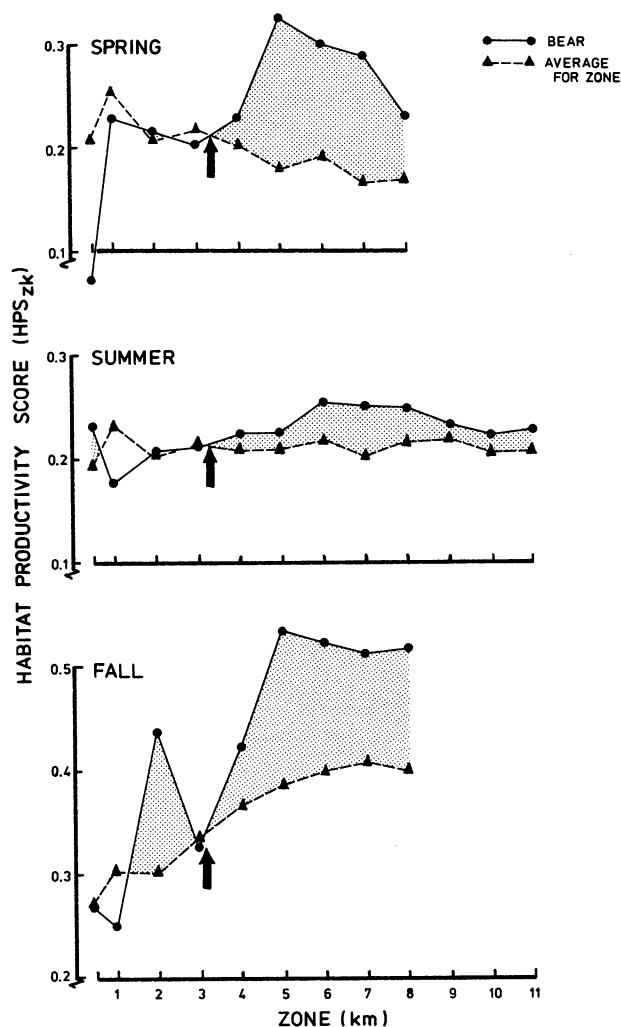


Fig. 8. Average habitat productivity score for bear location and grid-point scan areas, by season, for development 15-km analysis zones.

Differences in management history were evident between adult females and subadult males tending to range closer and farther than 7 km of developments. Mean per-year trapping of the 3 bears ranging closer to developments ($\bar{x} = 0.38$, $S_x = 0.20$) was 4 times that of the other 10 bears ($\bar{x} = 0.10$, $S_x = 0.13$). The difference in population location for the 2 groups of bears was significant (Mann-Whitney U-test; $P = 0.032$).

15-km Analysis, Summer, Adult Females

We conducted a secondary analysis specific to adult females ($N = 8$) during summer to quantify any

apparent avoidance of roads and developments by this class. This analysis was conducted because (1) human visitation in Yellowstone Park was greatest during summer, (2) substantial apparent avoidance of roads (1,500-m analysis) and developments (15-km analysis) by all bears was evident for this season, and (3) survival of adult females is considered critical to long-term viability of the Yellowstone grizzly bear population (Knight and Eberhardt 1984, 1985).

Observed adult female zone use differed significantly from expected around developments, but not along roads (Fig. 12). The pattern of adult female zone use around developments was similar to that of

ROADS

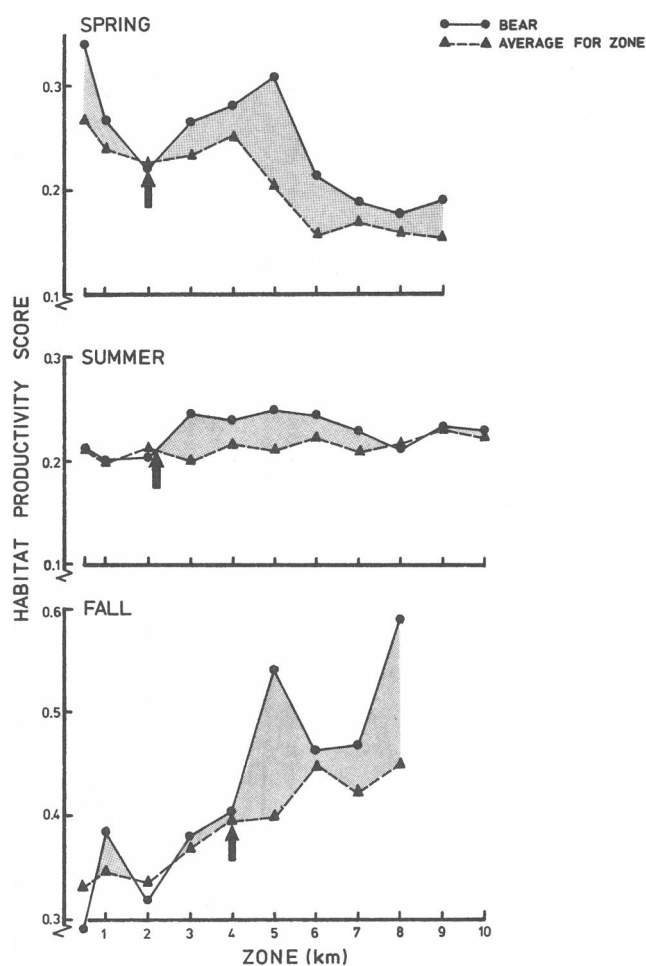


Fig. 9. Average habitat productivity score for bear location and grid-point scan areas, by season, for road 15-km analysis zones.

Table 2. Proportionate representation of cohort aerial telemetry locations in zones progressively outward from developments for spring, summer, and fall. Coefficient of variation (C.V.) for zone proportions for cohorts for each season is also given. Zone numbers correspond to outer zone boundary in km from developments

Outer zone boundary (km)	Females			Males	
	Adults		Subadults	Adults	Subadults
	With cubs ^a	Other			
Spring					
1	0.17	0.66	0.17	0.00	0.00
3	0.39	0.34	0.06	0.12	0.08
5	0.11	0.39	0.21	0.09	0.20
7	0.14	0.39	0.15	0.23	0.09
9	0.12	0.44	0.08	0.29	0.06
11	0.14	0.27	0.17	0.32	0.08
13	0.16	0.39	0.04	0.26	0.14
15	0.05	0.33	0.05	0.54	0.03
C.V.	0.62	0.29	0.57	0.67	0.73
Summer					
1	0.24	0.20	0.12	0.16	0.28
3	0.12	0.31	0.28	0.12	0.16
5	0.09	0.28	0.42	0.13	0.07
7	0.18	0.27	0.21	0.12	0.22
9	0.15	0.35	0.18	0.16	0.16
11	0.19	0.45	0.12	0.14	0.09
13	0.12	0.38	0.09	0.33	0.17
15	0.38	0.18	0.09	0.25	0.09
C.V.	0.50	0.30	0.60	0.43	0.46
Fall					
1	0.06	0.13	0.19	0.12	0.50
3	0.14	0.31	0.24	0.19	0.12
5	0.30	0.31	0.15	0.18	0.06
7	0.21	0.41	0.10	0.19	0.10
9	0.11	0.26	0.24	0.27	0.13
11	0.16	0.18	0.20	0.29	0.16
13	0.17	0.25	0.10	0.32	0.17
15	0.14	0.10	0.24	0.49	0.03
C.V.	0.44	0.42	0.33	0.45	0.92

^a Cubs-of-the-year.

all bears pooled; observed use was substantially less than expected from 3 to 5 km and 7 and 8 km.

Average adult female location habitat productivity scores were less than the zone average from 0 to 2 km along roads and 0 to 3 km around developments (Fig. 13). This negative deviation for adult females was greater than that for all bears.

The effect of roads and developments on adult female habitat use was calculated from summer adult female telemetry locations. This calculation took into account deviation of observed from expected levels of use and deviation of mean bear location habitat productivity scores from zone means, within a specified "zone of influence," in this case 4 km along roads and 6 km around developments. Zone of in-

fluence corresponded to zones bordering a road or development within which use was less than expected or bear location habitat productivity scores were less than or nearly equal to zone averages (Weaver *et al.* 1986). An estimate of total road and development effects on adult female habitat use in Yellowstone Park was the product of proportionate zone of influence effect multiplied by zone of influence area as a proportion of the park total. Overlap of road and development zones of influence were taken into account. Calculation methodology is in the Appendix.

Results indicated that adult female habitat use in Yellowstone Park was 15.7% less than expected without the presence of roads and developments. If we assume that the adult female population was near 50

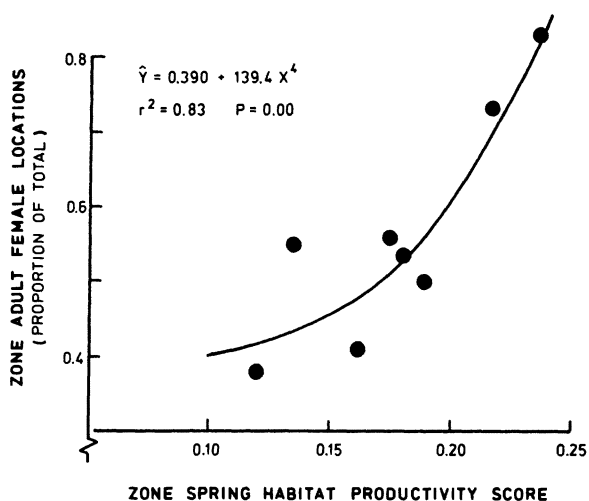


Fig. 10. Relationship of adult female locations to average habitat productivity score during spring for 15-km analysis zones; locations are expressed as a proportion of the zone total.

(Knight and Eberhardt 1984), that near 30 of these animals resided predominantly within the park, and that Yellowstone Park was near carrying capacity (Picton et al. 1986, Mattson 1987), then this effect translates into loss of habitat sufficient to support 4 or 5 adult females during summer.

DISCUSSION

Error and Bias

Some potential complications are associated with using zone widths of 100–300 m, as we did for our 1,500-m analysis. Aerial locations of telemetered bears may have errors greater than 100 m. Ground analysis of aerial locations by IGBST personnel suggested that a majority of our locations had errors less than 200 m. Many locations were by sighting and so were very accurate; a few locations were known to be as much as 1 km in error.

The consequences of this error to our analysis were probably minor even though a substantial number of bear locations undoubtedly occurred in zones other than indicated by aerial telemetry. However, most of the trade-off due to this error would be with adjacent zones. Because our primary objective was to analyze broad patterns, as much as 600 m in the 1,500-m analysis, we concluded that location error did not compromise interpretation of results.

Simple interpretation of results was more likely complicated by biases inherent in aerial location of telemetered animals. Most of our locations occurred during morning hours and grizzly bear are night-active in the Yellowstone area, especially during summer (Schleyer 1983, Harting 1985). Because of this

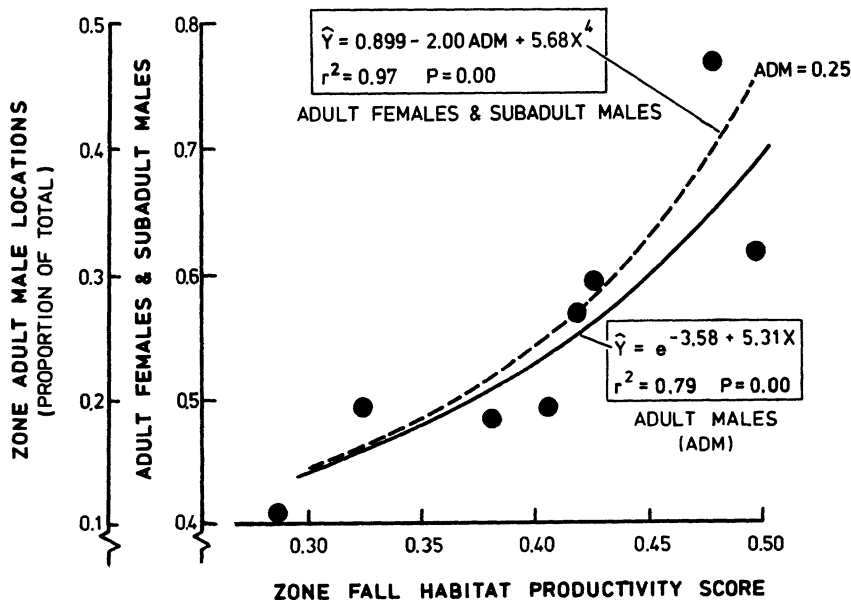


Fig. 11. Relationship of adult male, adult female, and subadult male locations to average habitat productivity score during spring for 15-km analysis zones; locations are expressed as a proportion of the zone total.

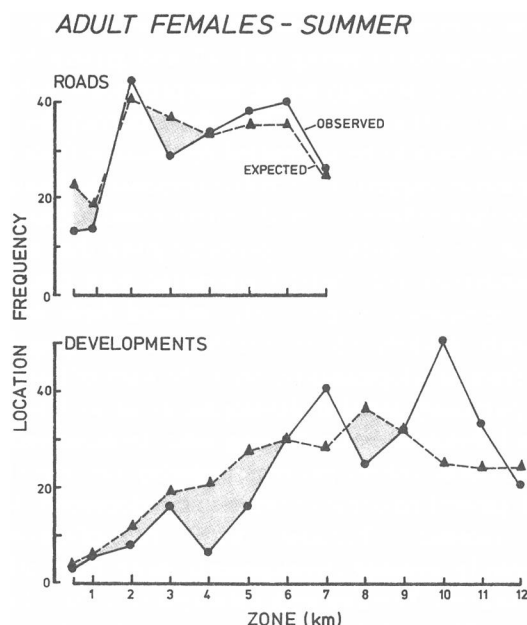


Fig. 12. Observed (adult female bear location) and expected (weighted grid-point) summer frequencies for road and development 15-km analysis zones.

diel bias, observed habitat use close to roads and developments may not reflect actual habitat use. Bears could have made additional night-time use of adjoining areas. This does not discredit the fact that bears were apparently avoiding humans during the day; however, actual was probably greater than calculated summer habitat use for adult females within road and development zones of influence.

Bear Behavior

Avoidance of humans by bears was interpreted as taking 2 forms: (1) disruption of foraging activities that tend to maximize use of the most productive habitat within a zone; and (2) outright avoidance of areas near front-country human facilities. Disruption of otherwise efficient foraging strategies was inferred primarily from bear location habitat productivity scores less than or nearly equal to zone averages, and outright avoidance from observed bear use less than expected in zones adjoining or near by human facilities.

We assumed that the costs of avoidance evident by aerial telemetry locations were greater during spring and fall compared to summer. This assumption resulted from the tendency for grizzly bears to be more day-active during spring and fall compared to summer in the Yellowstone area (Schleyer 1983, Harting

1985). Thus, daytime avoidance attributed to human facilities during spring and fall probably reflected a greater behavioral response and associated stress or energy related costs compared to summer. Spring and fall also corresponded to potentially critical periods of post-den emergence and prehibernation hyperphagia. The post-den emergence period is thought to be especially important to adult females in the Yellowstone area (Mattson 1987); prehibernation hyperphagia was probably important to all cohorts (Nelson et al. 1983, Nelson et al. 1984, Mattson 1987).

Spring.—Adult females occupied the most productive spring habitat; proportionate zone distribution of this cohort was positively related to zone distribution of spring productivity scores. Thus, because spring productivity was highest near roads and developments, adult females tended to occupy habitat near these facilities.

Adult males tended to be proportionately distributed farther from developments during spring. This distribution probably did not reflect avoidance of developments because spring distribution of adult males was more likely an artifact of previous fall distribution. Spring and fall proportionate representation of adult males was strongly correlated ($r = 0.95$, $P = 0.000$).

Bears also apparently avoided humans during spring. Our data suggest that during daylight hours bears tended to avoid an area averaging 500 m along

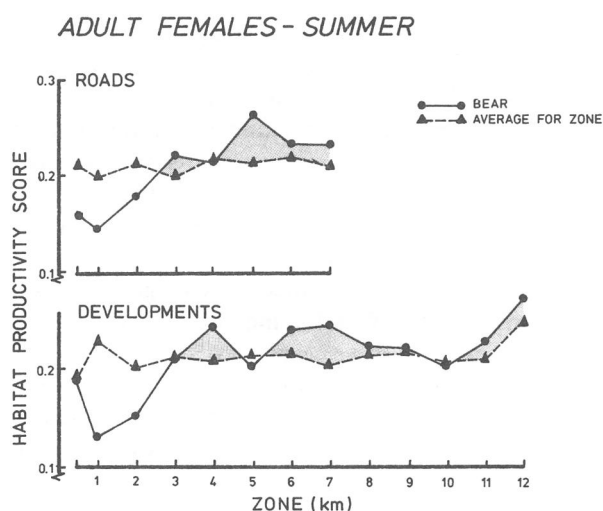


Fig. 13. Average summer habitat productivity score for adult female bear location and grid-point scan areas, for development and road 15-km analysis zones.

roads. Spring response to developments was evidenced by disruption of foraging out to 3 km. Other data collected while surveying spring bear use of ungulate carcasses in the Old Faithfull area (Mattson and Henry 1987) showed that only 6%–7% of carcasses within 5 km of the development were used by bears; 50%–100% of carcasses beyond 5 km had been used by bears. These observations were consistent in 1985 and 1986. Taken together, this analysis and the work of Mattson and Henry (1987) suggest a potentially strong avoidance of developments by grizzly bears during spring.

Summer.—Grizzly bears tended to avoid an area averaging 500 m along roads during summer. As during spring, the avoidance more likely occurred during daylight hours. Unlike spring, daytime disruption of foraging out to 2 km of roads was also evident. These 2 phenomena suggest a slightly stronger daytime bear response to roads during summer compared to spring. This is consistent with much higher vehicle traffic levels during summer.

During summer no spatial avoidance of developments was apparent for zones out to 2 km. Bear use was less than expected for zones 2–5 km and 7–9 km from developments; disruption of foraging was also apparent out to 3 km. This relatively complex pattern can be understood by looking at zone distribution of telemetry locations for individual bears. The 3 peaks in observed vs. expected use could be explained by a greater number of bears concentrating their activity in corresponding zones. Although most bears ranged across all zones, individuals could be distinguished by a greater tendency to range nearby (< 5 km), at intermediate distances (5–7 km), and far from (> 7 km) developments during summer.

Several interpretations of summer bear distribution with respect to developments were possible. However, we favored the following: bears tending to range closest to developments (< 5 km) were very likely habituated to humans and human facilities. Further, the apparent greater number of management trappings among adult females and subadult males suggests that many of these bears were food conditioned. Bears tending to range beyond 7 km of developments were probably less often habituated to humans or conditioned to human foods located at developments. Significantly, 30% of Yellowstone Park was within 7 km of a front-country campground or development.

The summer pattern of bear habitat use around developments could have resulted from bear response to humans and human foods. Habitat productivity

was more evenly distributed across zones during summer compared to spring and fall and grizzly bears did not key as strongly on the most productive habitat across or within zones. Thus, the tendency for individual bears to be segregated by distance from developments suggests differential response to humans rather than differential productivity-based habitat selection. This is even more probable given that zones of “under-utilized” habitat alternated with zones of peak occupancy progressively outward from developments. A likely inference is that bears ranging farther from developments tended to be wary of humans and purposely avoided developments as well as the more habituated bears ranging near developments.

Individual cohort patterns underlay the hypothesized general response of bears to developments during summer. Females with cubs-of-the-year apparently avoided developments more than other bear cohorts. Females with cubs appear to have been in a double-bind during summer, avoiding humans and other adult bears. Subadults also apparently avoided adult females during summer. Furthermore, subadult locations comprised a larger portion of total locations within vs. beyond 7 km of developments. Thus, subadults appear to have ranged closer to developments during summer in part because they tended to avoid adult females. The response of typically low status (subadults) or security-conscious (females with cubs) cohorts to adult females during summer may have partly reflected a response to adult males; adult males would have been seeking out estrus females and would, consequently, be associated with them (Craighead and Mitchell 1982, Schleyer 1983).

Fall.—Adult males tended to occupy the most productive fall habitat; proportionate zone locations of adult males were related to zone fall productivity scores. Adult females and subadult males, when allowed access, also tended to occupy productive fall habitat. However, avoidance of or displacement by adult males apparently outweighed habitat preference among these 2 cohorts during fall. These relationships would be expected with hyperphagia (Nelson et al. 1983, Nelson et al. 1984) and from previous observations of bear cohort interactions at garbage disposal sites and spawning streams (Hornocker 1962, Egbert and Stokes 1976).

Our data suggested that grizzly bears tended to avoid an area averaging 3 km along roads during fall and that foraging tended to be disrupted out to 4 km. This response of bears to humans on roads during fall is problematic, given that vehicle traffic dropped

markedly in Yellowstone Park around the 1st week of September (Yellowstone Natl. Park, unpubl. data). Fall zone productivity scores were lowest within 5 km of roads and average forest cover was comparatively low out to 4 km. Lack of cover combined with comparatively unproductive habitat may have caused the observed comparatively low levels of daytime bear use along roads during fall.

During fall a pattern of daytime bear use similar to that of summer was evident around developments. Our interpretation of this pattern was similar to that of summer: habituated bears tended to occupy zones within 3 km and especially within 1 km of developments. Use greater than expected within 1 km likely reflected the presence of food-conditioned habituated bears. If the presence of habituated bears accounts for bear use greater than or nearly equal to that expected out to 1 km, then bear use less than expected in the broader area out to 4 km could be attributed to avoidance of developments by other bears and lack of human-related foods so far distant from developments. The area out to 4 km also coincided with low average productivity scores and percent forest area. These habitat factors would have probably contributed to, rather than mitigated, a daytime avoidance response by grizzly bears.

CONCLUSIONS

Three phenomena were evident from our analysis: (1) bears selecting more productive habitat, (2) bears avoiding bears, and (3) bears avoiding humans. Our analysis further suggested that the relative strength of these phenomena varied with season and cohorts. During spring females apparently selected highly productive habitat and secondarily, responded to the human presence. Adult males were apparently more indifferent to habitat conditions and further removed from humans. During summer strong selection for highly productive habitat was not evident by any cohort; and avoidance of humans and other bears more evident. Subadults and females with cubs were apparently most likely to avoid other bears, and females with cubs most likely to avoid humans. During fall all cohorts were probably strongly motivated toward selection of highly productive habitat. Even so, adult males apparently displaced other cohorts from the most productive habitat. Secondarily, bears also avoided humans, but in areas inherently less productive. Because adult females and subadults tended to be distributed closer to roads and developments

and accounted for a large portion of locations especially during spring and fall, these cohorts were likely responsible for a large part of observed avoidance of humans.

Avoidance of humans using roads and developments in Yellowstone Park probably exacted a cost on the grizzly bear population. Adult females and subadults apparently bore a disproportionate part of this cost. Knight and Eberhardt (1984, 1985) have suggested that viability of the Yellowstone grizzly bear population is in large part contingent on survivorship of adult females. Mattson (1987) has also suggested that adult females, unlike adult males, experienced an ongoing energetics crisis; weights, mortality, and fecundity of adult females were strongly related to year-to-year and geographic variation in habitat productivity. Avoidance primarily of developments during spring and roads and developments during fall aggravated what was already an apparently marginal energetic situation for adult females. Thus, we conclude that avoidance of roads and developments by grizzly bears in Yellowstone Park probably resulted in poorer condition adult females and, consequently, higher mortality rates and lower fecundity for the cohort. However, we did not determine the extent of this effect.

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APPENDIX

- Er_{ik} : expected bear relocation frequency in zone i for season k in road 15-km analysis zones (Ed_{ik} for development zones).
- Or_{ik} : observed bear relocation frequency in zone i for season k in road 15-km analysis zones (Od_{ik} for development zones).
- Dr_{zk} : displacement coefficient for influence zone z for season k with respect to roads (Dd_{zk} with respect to development).
- Pr_z : proportion of total park area within influence zone z (Pd_z with respect to developments).
- TD_{zk} : total displacement for zone z during season k .
- $AHQr_{ik}$: average grid HPS_{ik} for zone i during season k in road 15-km analysis zones outside displacement effect ($EHQd_{ik}$ for development zones).
- $OHQr_{ik}$: observed HPS_{ik} for zone i during season k in road 15-km analysis zones outside displacement effect ($OHQr_{ik}$ for development zones).
- $ADJr_k$: adjustment factor for $AHQr_{ik}$ for season k in road 15-km analysis zones within displacement effect ($ADJd_k$ for development buffer zones).
- $DHQr_{zk}$: depression coefficient for influence zone z during season k with respect to roads ($DHQd_{zk}$ with respect to developments).
- DCr_{zk} : displacement/depression coefficient for influence zone z during season k with respect of roads (DCd_{zk} with respect to developments).
- $TD(hq)_{zk}$: total displacement/depression for influence zone z during season k with respect to roads ($TD(hq)d_{zk}$ with respect to developments).
- OLP : proportionate overlap between road and development and zones of influence.
- $TDrd(hq)_{zk}$: total displacement/depression for influence zone z during season k due to roads and developments.
- $Dr_{zk} = (\sum(Er_{ik} - Or_{ik}))/\sum Er_{ik}$ for negative sums only, within influence zone z .
- $TDr_{zk} = DR_{zk} \times Pr_z$
- $ADJr_k = 1 + ((\sum(OHQr_{ik} - AHQr_{ik}))/\sum AHQr_{ik})$ for road 15-km analysis zones outside displacement effect.
- $DHQr_{zk} = \sum((ADJr_k \times AHQr_{ik}) - OHQr_{ik})/\sum(ADJr_k \times AHQr_{ik})$ for road 15-km analysis zones with displacement.
- $DCr_{zk} = DHQr_{zk}(1 - Dr_{zk}) - Dr_{zk}$
- $TD(hq)_{zk} = DCr_{zk} \times Pr_z$
- $TDrd(hq)_{zk} = (1 - OLP)TD(hq)r_{zk} + TD(hq)d_{zk}$