

Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975 – 1989

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Abstract: We investigated the distribution, diet, and reproduction of grizzly bears (*Ursus arctos*) in the Yellowstone ecosystem that fed on cutthroat trout (*Oncorhynchus clarki*) spawning in streams tributary to Yellowstone Lake. We hypothesized that availability of trout influenced all of these factors for bears in a large part of the Yellowstone grizzly bear recovery area. Depending upon sex, bears that fed on trout used 30–45% of the recovery area. These bears concentrated within 12 km of spawning streams year-round and within 2 km of streams during the spawning season, 1 May – 15 July, when trout-eating bears mostly consumed trout. Despite use of this high-quality food, trout-eating females were apparently less fecund than other females and lost a larger percentage of their dependent young. We speculate that these cub losses resulted from higher rates of intraspecific predation by bears aggregated at spawning streams. These aggregated bears were also vulnerable to human-caused mortality, most likely due to concentrations of humans within 2 km of spawning streams during the spawning season.

Résumé : Nous avons étudié la répartition, le régime alimentaire et la reproduction de l'Ours brun (*Ursus arctos*) dans l'écosystème de Yellowstone où les ours se nourrissent de Truites fardées (*Oncorhynchus clarki*) frayant dans les ruisseaux tributaires du lac Yellowstone. Nous avons envisagé l'hypothèse selon laquelle la disponibilité des poissons a une influence sur toutes ces variables dans une grande partie de la zone de récupération des ours à Yellowstone. Selon leur sexe, les ours nourris de truites utilisaient 30–45% de la zone de récupération du parc. Les ours se tenaient à moins de 12 km des ruisseaux de fraye durant toute l'année et à moins de 2 km durant la fraye, du 1^{er} mai au 15 juillet, période au cours de laquelle les ours friands de truites mangeaient surtout des truites. En dépit de la haute qualité nutritive des poissons, les femelles nourries de truites étaient apparemment moins fécondes que les autres femelles et ont perdu un pourcentage plus élevé de leurs oursons. Nous croyons que la perte de ces oursons est attribuable à l'augmentation de la prédation intra-spécifique dans la zone de rassemblement des ours autour des ruisseaux de fraye. Les ours rassemblés étaient également plus vulnérables à la mortalité reliée à l'action humaine, probablement à cause de l'existence, durant la saison de fraye, de zones de forte densité humaine à moins de 2 km des ruisseaux de fraye. [Traduit par la Rédaction]

Introduction

Cutthroat trout (*Oncorhynchus clarki*) are a highly digestible high-energy bear food (Pritchard and Robbins 1990) and are of potential importance to grizzly bears. Salmonids are also, predictably, more underrepresented in fecal analysis than any other bear food, including ungulates (Hewitt 1989).

There is thus the potential for a consistent bias against representation of trout in bear feces and a corresponding tendency to underestimate their contribution to bears' diets.

Earlier work in the Yellowstone ecosystem of Wyoming, Montana, and Idaho (Reinhart and Mattson 1990) suggested that 61% of all known cutthroat trout spawning streams tributary to Yellowstone Lake were fished by bears during the spawning season, typically 1 May – 15 July. The number of streams fished by bears had furthermore increased by 3.3× in an 11-year period, with no known relationship to changes in the bear population. A minimum of 44 autonomous bears were estimated to have used these streams during 1987, when all spawning streams were sampled. Thus, despite the fact that cutthroat trout were relatively infrequent in bear feces from the Yellowstone ecosystem (Mealey 1980; Mattson et al. 1991), we postulated that spawning cutthroat trout from Yellowstone Lake influenced the behaviour and reproduction of a large portion of Yellowstone's grizzly bears.

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We test our general proposition by construing the influences of trout consumption in terms of (i) spatial aggregation of bears relative to spawning streams, (ii) temporal aggregation, especially relative to the spawning season, (iii) proportionate consumption of trout by bears when near spawning streams, (iv) relative use of habitat near these streams by adult females, and (v) differences in reproduction between females who ate trout and those who did not. We accordingly tested the following null hypotheses (with the rationale in parentheses):

- H1: The aggregate home range of radio-collared bears known to consume spawning trout had a standard radius relative to spawning streams that was equal to or less than the standard diameter of average life ranges for the respective sexes at large. (In theory, the radius of an aggregate range abutted on a feature like Yellowstone Lake would be equal to or less than the standard diameter of an individual range if trout were not attracting bears from a larger expected area.)
- H2: The relative frequency of adult female radio-relocations near spawning streams during the spawning season was equal to or less than the relative frequency of locations for males known to eat trout. (If females and males used trout with equal intensity, there should be no difference in relative concentration of radiolocations.)
- H3: The proportional distribution of radiotelemetry locations for all bears and bears known to eat trout was random with respect to spawning streams during the spawning season. (If spawning trout did not constitute an attractant, then there should be no relative concentrations of locations.)
- H4: When near spawning streams during the spawning season, bears ingested trout at frequencies that did not differ from the average among diet items ecosystem-wide. (If the frequency of trout consumption was no different from the average elsewhere in the grizzly bear range, there would be no basis for assuming that grizzlies were orienting to these areas specifically to eat trout.)
- H5: Age at first reproduction and the reproductive interval of adult females that ate trout were equal to or greater than, and litter size was less than, those of adult females that did not eat trout. (If the fecundity of trout-eating bears was equal to or less than that of females elsewhere, we could not conclude that consumption of trout had a dominating, positive effect on reproduction.)

These hypotheses relate to factors, such as temporal and spatial aggregation, that are particularly relevant to management. Thus, if bears from a disproportionately large area were known to eat spawning trout, concentrated around spawning streams during the spawning season primarily to eat trout, and constituted a disproportional number of adult females that were more fecund than expected, this would be a strong basis for concluding that cutthroat trout were an important resource for Yellowstone's threatened grizzly bear population, warranting special management.

Study area and methods

For our analysis we used the results of two studies, one based upon radiotelemetry sampling and another upon stream-side surveys. Details of the broader study area and methods for the radiotelemetry study are provided by Blanchard and Knight (1991) and Mattson et al. (1991), while details of the

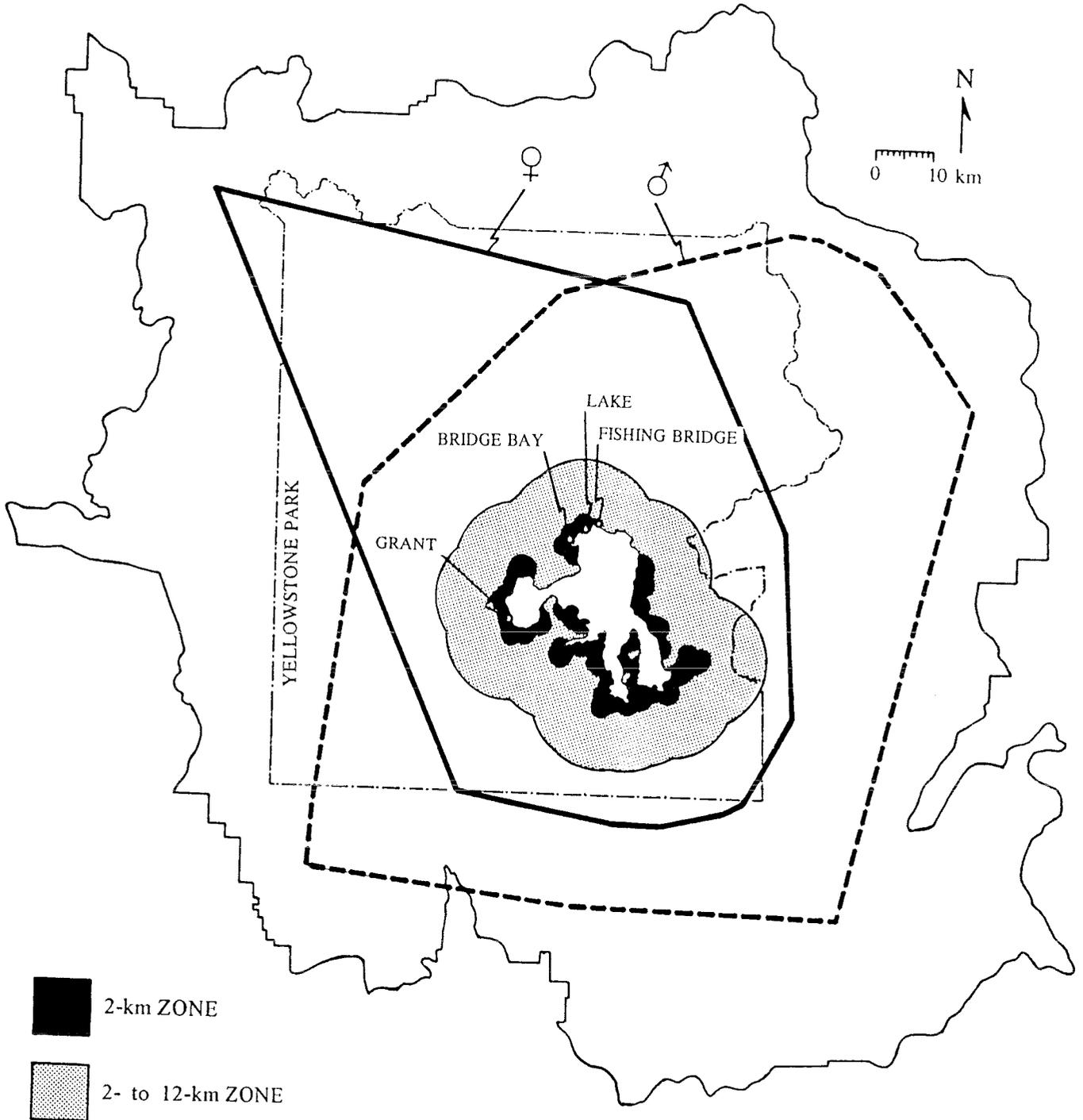
Yellowstone Lake tributaries study area and survey methods are provided by Reinhart and Mattson (1990). Both studies were located within the 23 300 km² that compose the Yellowstone grizzly bear ecosystem of northwest Wyoming, southwest Montana, and east Idaho. The area around Yellowstone Lake is high elevation (>2350 m), cold (average annual temperature 0°C), and predominantly (>75%) forested (Despain 1990). The lake itself is deep (mean depth 42 m) and exceptionally large (35 391 ha) for its elevation. The lake furthermore contains a large and unique population of cutthroat trout (*O. c. bouvieri*) (Varley and Gresswell 1988).

During stream-side surveys we collected information on stream characteristics, numbers of spawners, and level of bear use along 100-m stream reaches, as well as all bear feces encountered. These feces were subsequently analyzed for frequency and volume of diet items according to techniques described in Mattson et al. (1991). Before statistical analysis we used correction factors (Hewitt 1989) to account for differences between assayed fecal volume and expected ingested mass, and consequently we report our results as estimates of both ingested and defecated volumes. We used a multiple comparisons procedure for arcsine-transformed proportions analogous to Dunnett's test (Zar 1984) to test the hypothesis that cutthroat trout did not occur more frequently in feces collected around Yellowstone Lake than other major diet items in feces ecosystem-wide for the same season.

We used a geographic information system (GEOCALC) that was specifically programmed to analyze our radiotelemetry data for the spatial analysis. We digitized the lakeshore of Yellowstone Lake and all stream reaches of tributary streams known to be used by bears and calculated nearest distances to these streams for all radiotelemetry locations ($n = 7478$) in our 1975–1989 data set and for an equal number of random points. Bears that ate trout or had access to trout were identified on the basis of ≥ 1 radiotelemetry location within 500 m of a known spawning stream during the spawning season (1 May – 15 July). Most (87%) of this inferred use was corroborated by ground sampling of telemetry locations or by direct observation. We further distinguished adult females by those with ≥ 5 qualifying locations when we analyzed reproduction. We defined subadults as bears <5 years old that had been weaned and determined reproductive parameters (age at first reproduction, reproductive interval, and litter size) according to Knight and Eberhardt (1985).

We tested the equality of frequency distributions among non-ordered categories by the log-likelihood (G) test, and used Fisher's exact test where $df = 1$ or where cell sample sizes did not meet minimum criteria for the G test (>20% had expected frequencies <5 or 1 cell had an expected frequency <1) (Zar 1984). For ordered distance categories, we tested for goodness of fit between observed and expected frequencies by the Kolmogorov–Smirnov (K-S) D test. Differences between proportions within individual categories were tested using Bonferroni confidence intervals (Neu et al. 1974; Byers et al. 1984). We used the iterative approach described by Mattson et al. (1991) and Mattson et al. (1992a) for testing randomness or equivalency of radio-relocation frequency distributions among zones defined by distance to a spawning stream. According to this approach, zones were defined on the basis of visual inspection of patterns as well

Fig. 1. Yellowstone Lake and areas within 2 km and 2–12 km of tributary cutthroat trout spawning streams known to be used by Yellowstone grizzly bears, 1975–1989. Aggregate ranges of male (♂) and female (♀) bears known to use trout are shown, along with the boundary of Yellowstone National Park and the outermost boundaries of Bear Management Units defining the area within which the distribution of Yellowstone's grizzlies is tracked for judging population recovery (U.S. Fish and Wildlife Service 1993).



as the area where trout-eating bears accounted for > 50% of all radiolocations. Patterns were confirmed by the fit of least-squares regression to proportions in different zones.

We calculated aggregate range sizes by the minimum convex polygon (MCP) method, to allow comparison with previous results obtained using the same technique (Blanchard and Knight 1991). Our area calculations did not include Yellowstone Lake (35.4 km²). We determined whether the standard radii, by sex, of the aggregate ranges for bears that

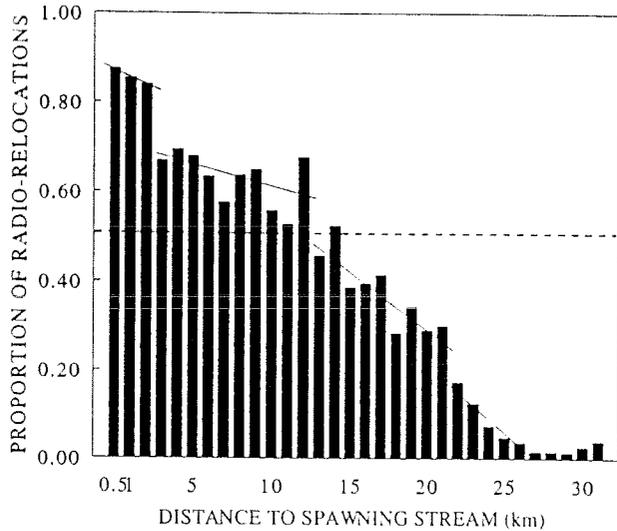
ate spawning trout fell within 95% confidence limits of mean life range diameters of bears not known to eat trout. Life ranges were taken from Blanchard and Knight (1991).

Results

Home range

Aggregate MCPs of male and female grizzlies that ate spawning cutthroat trout were 10 053 and 6280 km², corresponding

Fig. 2. Year-round radio-relocations of grizzly bears that used spawning cutthroat trout, as a proportion of total grizzly bear relocations, according to the distance (km) to spawning streams, Yellowstone Lake, 1975–1989. Different lines fit by least-squares regression demarcate alternating plateaus and steps in the relative frequency distribution at 2, 12, and 21 km.



to 44.7 and 28.5% of the total Yellowstone grizzly bear Recovery Area (23 300 km²), respectively (Fig. 1). The standard radius of the males' aggregate range (56.6 km) did not fall outside of 95% confidence intervals (CI) (29.7–111.0 km) for the mean life range standard diameter for males (70.3 km). Conversely, the standard radius of the females' aggregate range (44.7 km) was greater than the upper 95% CI (34.7 km) for the mean life range standard diameter for females (31.0 km).

Consistency of use

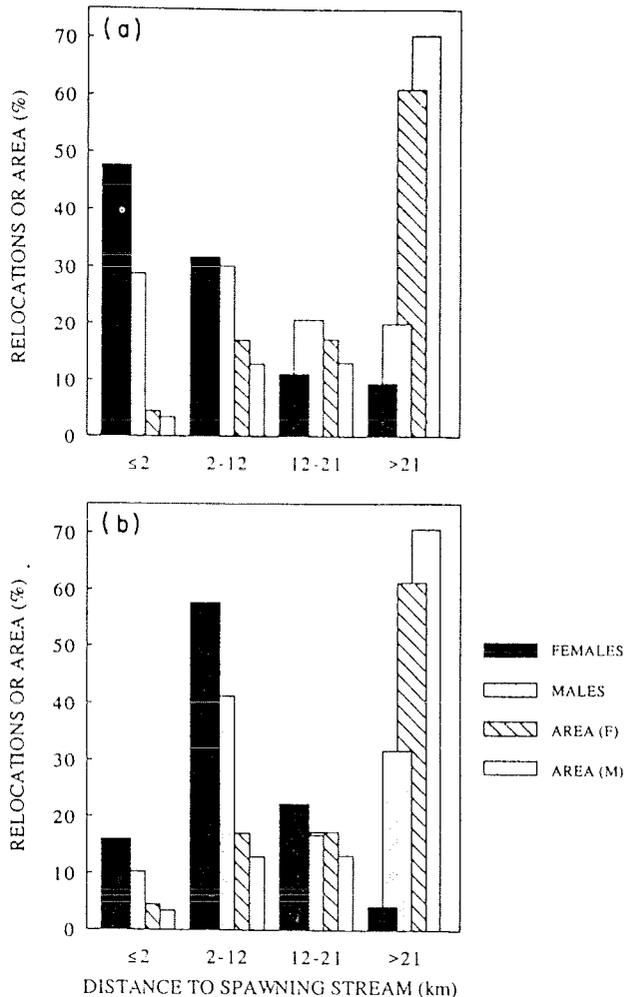
Compared with males, females that ate trout at least once tended to consume trout during a higher percentage of the years that they were monitored (62.5 versus 87.5%, respectively; Fisher's exact test, two-tailed, $P = 0.093$, $n = 24$ bear-years each) and had proportionately more radio-relocations within 2 km of spawning streams during the spawning season (28.8 versus 47.3%; Fisher's exact test, two-tailed, $P = 0.0002$, $n = 296$ and 149, respectively). This disparity in "use" years was not different from that expected by differences in aggregate range size between males and females ($df = 1$, $G_c = 0.109$, $P = 0.74$), although there was a difference in intensity of use between the sexes, indicated by proportions of relocations in the 2-km zone ($df = 1$, $G_c = 35.1$, $P < 0.001$).

Distribution

Radiotelemetry locations of bears that ate trout accounted for a progressively smaller portion of total locations year-round as distance to spawning streams increased (Fig. 2). This decline was not uniform and exhibited steps alternating with plateaus at 2, 12, and 21 km distance. Trout-eating bears accounted for >50% and >80% of total locations within 12 and 2 km of spawning streams, respectively.

Distributions of radiotelemetry locations from trout-eating bears were not random with respect to either spawning streams or the broad distance categories defined above (2, 12, and 21 km), and differed between males and females and between

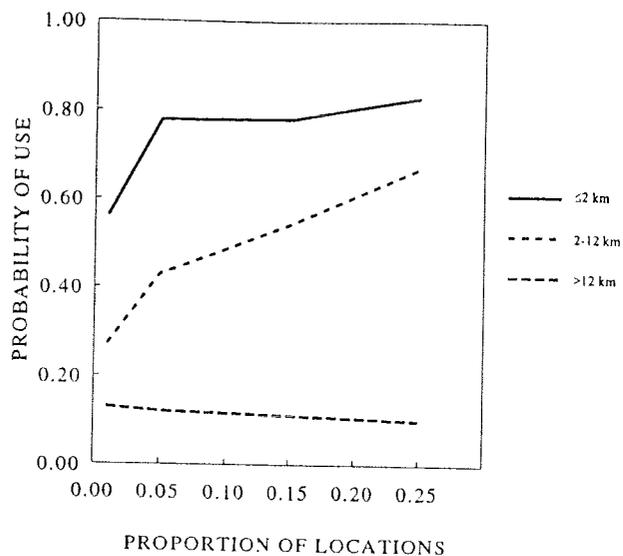
Fig. 3. Percentage of total radio-relocations from grizzly bears that ate spawning cutthroat trout by distance from spawning streams and by sex, and percentage of the total area within distance categories, within 44.5 and 56.5 km of streams for females and males, respectively, for the spawning season (1 May – 15 July) (a) and for the remainder of the year (b).



spawning and nonspawning seasons (Fig. 3). Frequency distributions for males and females differed year-round and during both seasons (in all three cases $df = 3$, $G \geq 23.3$, $P < 0.0001$). Locations of females were relatively more frequent (1.65 \times) than those of males ($P \leq 0.05$) within 2 km of spawning streams during the spawning season, and more frequent within both the 2- and 12-km zones (1.55 \times and 1.39 \times , respectively) during the nonspawning season. Similarly, the frequency distributions of radiotelemetry locations for both males and females differed between spawning and nonspawning seasons ($df = 3$, $G = 30.8$ and 116.9 for males and females, respectively, $P < 0.0001$), primarily by a redistribution of both sexes between the 2 km and 2 to 12-km zones between the two seasons. The relative frequency of telemetry locations was 2.8–3.0 \times greater (for males and females, respectively) within the 2-km zone during the spawning season and 0.6–0.7 \times greater than the nonspawning season density within the 2- to 12-km zone.

Distributions of both male and female relocations differed from those expected by zone areas year-round and during

Fig. 4. Observed probability that an individual grizzly bear would use spawning cutthroat trout as a function of the proportion of total year-round radio-relocations <2, 2–12, and >12 km from spawning streams, Yellowstone Lake, 1975–1989.



the spawning and nonspawning seasons ($K-S D_{max} \geq D_{\alpha}$, $P = 0.001$, in all three cases). Expected distributions among zones were calculated only for areas potentially occupied by trout-using bears, within 44.5 and 56.5 km of streams for females and males, respectively. Females and males used areas within 12 km of spawning streams more than expected ($P \leq 0.05$) during the spawning season. During the nonspawning season, males continued to use areas < 12 km from spawning streams more than expected, while females used areas out to 21 km more than expected. Females were more concentrated than males in the 2-km zone during the spawning season ($10.8\times$ versus $8.6\times$ expected use), but their concentration was similar to that of males in the 2-km and 2- to 12-km zones during the nonspawning season ($3.6-3.4\times$ for females versus $3.1-3.2\times$ for males).

We were also interested in the potential effects of spawning trout on bear distributions ecosystem-wide. The 12-km zone of influence for spawning streams composed 17.8% of the total area containing bear relocations. The relative frequencies of all bear locations differed from that expected by the area ≤ 12 km from spawning streams and the area beyond that distance to the limits of bear distribution, year-round and for both the spawning and nonspawning seasons ($K-S D_{max} > D_{\alpha}$, $P = 0.0001$ in all three cases). The relative frequencies of bear locations were 1.36 , 1.38 , and $1.35\times$ greater than expected ($P \leq 0.05$) by the area within 12 km of spawning streams year-round and during the spawning and nonspawning season, respectively.

Probability of use

The probability that a bear would use spawning cutthroat trout varied with the proportional distribution of its year-round relocations in the zones ≤ 2 , 2–12, and >12 km from spawning streams (Fig. 4). Probability of use remained more or less constant (0.78–0.83) once the proportional distribution of locations was ≥ 0.05 within the 2-km zone. Con-

versely, the proportional distribution of locations beyond 12 km alone had relatively little relationship to the probability of bears eating spawning trout.

Diet

After adjusting for the difference between defecated volume and ingested mass, it was clear that bears mostly consumed trout while using riparian habitats along Yellowstone Lake streams during the spawning season (Table 1). Our estimate of relative ingested mass was $5.6\times$ greater than the estimated fecal volume of trout (91.8 versus 16.5%). Volumetric defecation of trout was relatively constant among the years 1985–1987, and varied primarily with defecation of graminoids. The relative frequency of trout in feces collected along spawning streams (38.1%) was greater than the relative frequency of six other major diet items and only lower than the relative frequency of graminoids in feces collected ecosystem-wide during the spawning season (Dunnnett's test using angular transformations, $P \leq 0.05$). Similarly, the relative frequency of trout in stream-side feces was greater than the upper 90% CI (35.7) for mean angular transformations of relative frequencies of major diet items in feces ecosystem-wide.

Reproduction

We compared relevant reproductive parameters, including percent mortality of dependent young, litter size (1, 2, 3), age at first reproduction (≤ 5 , 6, ≥ 7 years), and reproductive interval (≤ 2 , ≥ 3 years) of females that did and did not eat spawning trout. When all females were included, only age at first reproduction tended to differ between females that did and did not eat trout (Fisher's exact test, two-tailed, $P = 0.060$), primarily because fewer trout-eating females first reproduced at age 6. When we considered trout-eating females with five or more locations near streams during the spawning season (deleting two females with only one qualifying location), all parameters except reproductive interval differed between females that did and did not eat spawning trout. The percentage of young dependent upon trout-eating females that were thought to have died was larger (36.4%) than that of dependent young of other females (12.1%) (Fisher's exact test, two-tailed, $P = 0.050$, $n_1 = 11$ and $n_2 = 116$ for trout-eating and other females, respectively). Similarly, first-recorded litter sizes were more often one (43.0 versus 9.6%) and less often three (0.0 versus 32.7%) for trout-eating females than for other females (Fisher's exact test, two-tailed, $P = 0.030$, $n_1 = 7$, $n_2 = 52$). All recorded ages at first reproduction were ≥ 7 years for trout-eating females compared with 19% of recorded ages for other females (Fisher's exact test, two-tailed, $P = 0.035$, $n_1 = 3$, $n_2 = 21$).

Discussion

Sex-based differences

We concluded that among trout-eating bears, females used the vicinity of streams during the spawning season more consistently and intensively than did males and, as a consequence, we rejected hypothesis H2. Much of this discrepancy can be explained by disparities in range size between the sexes. However, this did not negate our primary conclusion that, on average, individual females made greater use of spawning cutthroat trout than did individual males. This

Table 1. Relative volumes of major diet items in bear feces collected along streams tributary to Yellowstone Lake during the spawning season, by year, 1985–1987, and pooled relative frequencies and estimated ingested volumes of items for all years.

Diet item	% fecal volume			Pooled (1985–1987)	
	1985	1986	1987	% frequency	% ingested vol. ^a
Trout	19.0	25.8	12.8	38.0	91.8
Mammals	3.7	4.6	5.3	10.3	3.5
Birds	0.0	0.8	0.1	0.6	0.0
Ants	1.5	4.2	0.9	10.0	0.3
Forb foliage	13.3	14.8	14.8	27.9	1.0
Roots	0.7	0.0	0.2	0.3	0.1
Graminoids	43.2	32.4	56.4	76.2	3.0
Sporophytes	8.7	6.6	5.8	13.3	0.2
Fleshy fruits	0.8	0.8	0.1	0.9	0.0
Pine seeds	0.0	0.4	0.0	0.3	0.0
Sample size	143	124	404	671	

^aRelative ingested volume of the *i*th item (IV_i) was estimated as $IV_i = (n_i \times MPC_i \times SCF_i) / \Sigma IV_i$, where n_i is the number of scats in which the *i*th item occurred, MPC_i is the mean percent volume of the *i*th item in these scats where it occurred, and SCF_i is the scat correction factor appropriate for the *i*th item.

conclusion is supported by previous results from Yellowstone, including estimates by Reinhart and Mattson (1990) based on analysis of tracks along spawning streams, showing that females with dependent young accounted for percentages of autonomous bears (32–42%) much larger than expected from the estimated proportion of females with young in the population (19%, assuming a 3-year reproductive interval; U.S. Fish and Wildlife Service 1993).

Distribution

Cutthroat trout spawning in tributaries to Yellowstone Lake were potentially eaten by females occupying ca. 30% and males occupying ca. 45% of the Yellowstone grizzly bear recovery area. This zone of potential influence was $1.44 \times$ larger than expected for females by the lifetime range sizes of females not known to use trout. This disparity was attributable either to larger life-range sizes for trout-eating females and (or) positive attenuation of ranges with respect to spawning streams. We could not explicitly test these hypotheses because we did not have a sufficiently large sample of trout-eating individuals with multi-annual ranges. However, our results were sufficient grounds for rejecting hypothesis H1. Furthermore, they support the hypothesis that spawning trout were potentially used by females in a large fraction of habitat occupied by grizzly bears, and that this area of potential influence was disproportionately large. Similarly, if year-round use of areas ≤ 2 km from spawning streams exceeded a nominal amount (5% of the total), there was a high probability ($>75\%$) that an individual bear actually ate spawning trout.

The distribution of trout-eating bears was clearly not random with respect either to spawning streams or to zones of potential influence associated with these streams, so we rejected H3. Year-round locations of trout-eating bears were concentrated ($8.6–10.8 \times$ those expected) ≤ 2 km from spawning streams during the spawning season. Seasonal differences were primarily characterized by increased use of the 2- to 12-km zone during the nonspawning season, leaving

78–84% of aggregate ranges potentially occupied by trout-eating bears > 12 km from spawning streams (for females and males, respectively) relatively unused year-round. Spawning streams and their associated habitat complex thus exerted the greatest influence on distributions of trout-using bears as well as bears ecosystem-wide in an area ≤ 12 km. There was an additional zone of influence, ≤ 2 km, that characterized the spawning season.

On an ecosystem-wide basis, use of areas ≤ 12 km from spawning streams (17% of the recovery area) by all bears was $1.36 \times$ greater than expected on the basis of random occupancy. This pattern could have several causes other than consumption of spawning trout, including bias of trapping and relocation efforts towards spawning streams, attraction of bears to other high-quality feeding opportunities associated with riparian areas, or concentration of traveling bears along the barrier posed by Yellowstone Lake. However, these results could also be explained by a local increase in "carrying capacity" attributable to the availability and consumption of spawning trout. We cannot confidently reject any of these explanations and suspect that all may have contributed to the greater than expected use near spawning streams.

Diet

Bears could have aggregated near spawning streams to use other spatially correlated habitat features such as riparian vegetation. Graminoids as well as forbs and sporophytes such as horsetail (*Equisetum arvense*), elk thistle (*Cirsium scariosum*), and dandelion (*Taraxacum* spp.) were consumed by bears in riparian habitats (Mattson et al. 1991). Peak digestibility and use of these foods by bears were also more or less synchronous with cutthroat trout-spawning runs (Mattson et al. 1991). However, our corrected analysis of bear feces from riparian corridors clearly suggested that during all 3 sample years most ($>90\%$) of the bears' diet during the spawning season was trout. Trout consumption was also more frequent near streams than expected from con-

sumption of all other major diet items except graminoids ecosystem-wide.

Incidental observations corroborate this orientation of grizzly bears towards trout during the spawning season. On one occasion the principal author observed a bear catch and partially consume ($\bar{x} = 42\%$) 24 (ca. 0.45 kg) fish within 41 min. Although this was not a sustained mean rate of consumption, and cutthroat trout are smaller than coastal anadromous salmon (*Oncorhynchus* spp.), the volume implicit in this rate is comparable to that of 0.75–3.5 salmon/h observed for coastal brown bears by Egbert and Stokes (1976). Even though there were limitations to our fecal sample because we did not collect feces >500 m from a stream, our results lead us to reject hypothesis H4. They also support the hypothesis that trout were a major food of most bears ranging within 2 km of spawning streams during the spawning season.

The aggregation of Yellowstone grizzly bears near cutthroat trout spawning streams during the spawning season and their concurrent focus on trout consumption are congruent with the results of bear studies carried out elsewhere. Bears along the North Pacific rim consistently aggregate along spawning streams during spawning runs of anadromous Pacific salmon. Although fecal analyses have revealed only small volumes of defecated salmon (Clark 1957; Lloyd 1979), probably for the same reasons we pointed out in the Introduction, visual observations clearly suggested that a large portion of resident bears spent a substantial part of their time catching and eating fish during the spawning season (e.g., Bergman 1936; Shuman 1950; Clark 1959; Gard 1971; Stonorov and Stokes 1972; Egbert and Stokes 1976). Given this concurrence of results, we nonetheless expect that spawning Pacific salmon are more attractive to bears than cutthroat trout because of the greater energetic benefit implicit in their larger size (ca. 1.5 kg for the smallest, *Oncorhynchus gorbusha*, and ca. 8.3 kg for the largest, *O. tshawytscha* (Berg 1948)) and greater abundance.

Reproduction

Fish-eating females from our study first reproduced at a later age, had smaller litters, and lost a greater number of their dependent young than did other females in the Yellowstone recovery area. We clearly could not reject hypothesis H5. There may be grounds to anticipate that females which consumed trout would be in better condition than those that did not. However, this high-protein food may not be readily converted to the body fat that seems key to the fitness of female bears. We could not make any inferences about the dependence of observed levels of reproduction upon trout consumption, and tangentially, what the reproduction rates amongst trout-using bears would have been without access to spawning trout. Nonetheless, we could conclude that trout use did not fully compensate for any presumed habitat deficiencies impairing reproduction among females that ate trout compared with females that did not. Our results also lead us to hypothesize that trout use may have put dependent offspring at greater risk of predation by other bears.

Previous results from the Yellowstone area suggested that a disproportional part of the few documented bear-caused deaths occurred during the spawning season near cutthroat trout spawning streams, and that dependent young were the victims (Mattson et al. 1992b). The results of observational

studies at other bear aggregations, including bears fishing for Pacific salmon, also suggest that dependent young are at high risk, especially from adult males (Hornocker 1962; Stonorov and Stokes 1972; Egbert and Stokes 1976). These results further suggest that the extremely aggressive behaviour of females with young is a response to this risk. Logically, in a species where cannibalism is known to occur, aggregations of animals that place vulnerable individuals in closer juxtaposition to their potential intraspecific predators will likely result in greater mortality. Given that two documented cub losses by trout-eating females were caused by conspecifics during the spawning season, we speculate that the greater losses of dependent young by these females were largely attributable to the risks associated with aggregation. However, given that cub survival has an unknown or minor effect upon overall population growth (Knight and Eberhardt 1985), we are not sure how these cub losses affected population demography.

Implications for management

Yellowstone's grizzly bears concentrated near cutthroat trout spawning streams tributary to Yellowstone Lake during the spawning season, considering all bears and only bears that were known to use this resource. This concentration persisted during the nonspawning season, although in areas somewhat farther removed from streams. Females also accounted for a disproportionately large part of observed bear use near spawning streams. During the spawning season bears that were concentrated near streams appeared to primarily subsist upon trout. We thus have a good basis for concluding that spawning cutthroat trout were and are a resource that attracts and concentrates Yellowstone's grizzly bears and, therefore, that these fish and their spawning habitat warrant special management attention.

We did not have sufficient information to reliably estimate the survivorship of grizzlies using Yellowstone Lake's fishery compared with that of grizzly bears elsewhere in the recovery area. Nonetheless, between 1981 and 1990, 54% of all grizzly bear management trappings and 60% of all management removals in Yellowstone Park occurred at or near recreational facilities that were within 2 km of cutthroat trout spawning streams (i.e., Fishing Bridge, Lake, Bridge Bay, and Grant Village (Fig. 1)) (U.S. National Park Service 1993). Just as dependent young seemed to be more vulnerable to conspecific predators when grizzlies were aggregated near spawning streams, these aggregations near human facilities made grizzlies more vulnerable to conflict with humans and to death by human causes. Most (>75%) bear deaths recorded in the Yellowstone ecosystem have been caused by humans (Craighead et al. 1988). Human-caused mortality, in turn, largely determines the trajectory and prospects of this population (Knight and Eberhardt 1985; Mattson and Reid 1991). It logically follows that management of humans at recreational facilities within 2 km of Yellowstone Lake's spawning streams is important to the ultimate fate of the Yellowstone grizzly bear population.

These results also have potential applications outside our study area. Prior to their extinction, the inland population of grizzly bears occupying central and northern Idaho also used spawning salmonids (primarily chinook salmon (*O. tshawytscha*) (Davis et al. 1986)). These salmon are currently endangered and targeted for recovery, while at the same time this area is being considered for reintroduction of

grizzlies (U.S. Fish and Wildlife Service 1993). The potential influences and importance of a recovered salmon population to a reintroduced grizzly bear population are largely unknown. Our results offer a possible starting point for anticipating both the zones of influence for potential salmon spawning streams in Idaho as well as the extent of bear aggregations along these streams. While distributions of bears will likely vary according to the suite of available foraging options and habitats, our results suggest that most grizzly bears in central Idaho would use spawning salmon, and that they would aggregate along spawning streams during the spawning season. A computerized spatial application of our results could provide a more formal and explicit statement of this hypothesis and provide a basis for evaluating the potential importance of recovered salmon populations to reintroduced bears.

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