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

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Abstract: Aerial locations of radio-instrumented grizzly bears, digitized habitat map data, and digitized road and development map data were used to analyze effects of human activity associated with primary roads and developments on grizzly bear in Yellowstone National Park. Graphic and Chi-square analyses were used. Results suggested that occupancy of proximal habitat was reduced, otherwise efficient foraging strategies were disrupted, subadults were displaced towards roads and developments by more dominant bears, and the 0-3 km zone surrounding developments was an area of extremely high mortality risk for adult females. Road displacement and disruption were more pronounced on a micro (0-1500 m) scale; development effects were more pronounced on a macro (0-15 km) scale. Occupancy of habitat around developments by habituated neutral bears was corroborated. Habitat production sufficient to have supported three to four adult females was estimated to have been lost due to the effects of roads and developments. The zone of displacement was hypothesized to serve as a buffer between more wary bears and mortality risks of developments. Continued

sanitation of developments and control of motorized traffic during spring in prime bear habitat were suggested as management actions which could mitigate negative primary road and development effects.

SEVENTH INT. CONF. BEAR RES. MANAGE.

INTRODUCTION

Grizzly bear populations have almost universally been extirpated or put into decline after sustained contact with western civilization (Craighead and Mitchell 1982). This has primarily been a consequence of human-caused mortalities; habitat loss has been a secondary factor. Management and research have thus typically devolved to defining how much mortality and habitat encroachment a bear population can tolerate and remain viable. Key questions in such a process are (1) how do bears respond both generally and specifically to encounters with different densities and types of human activity, and (2) how does a given response influence mortality risk and habitat effectiveness for the individual animal or population.

Researchers have attempted to answer these questions. Bear-human encounters have been subject to analyses that associate human and site phenomena with encounter frequencies and human fates (Herrero 1976, Merrill 1978, Chester 1980, Jope 1985, Herrero 1985, and others). Other research has attempted to determine encounter effects on bears as a function of individual bear history, specific site, season, etc. (Schleyer et al. 1984, Haroldson and Mattson 1985). Still other studies have investigated or speculated on more general impacts of human

activities, primarily in association with logging or hydrocarbon exploration and development (Elgmork 1978, Harding and Nagy 1980, Schallenberger 1980, Zager 1980, Aune 1984, and others).

The effect of human activity concentrated at roads and developments on bears is an issue in Yellowstone Park. In excess of 2 million people visit the park each year during the same period that grizzly bears are active. Fifty percent of the park is within 8 km (5 miles) of a primary road and 11.5 km (7 miles) of a village or front-country campground. Furthermore, the Yellowstone grizzly bear population appears to be marginally viable (Knight and Eberhardt 1984 and 1985).

In this paper we address whether and to what extent primary roads and developments have affected grizzly bear in Yellowstone National Park. We further address how these impacts were manifest by mortality risk and habitat effectiveness.

STUDY AREA

The analysis area was constrained to Yellowstone National Park (Fig. 1), a management entity approximately 10,000 sq km in size. Elevations were predominantly between 2130 and 2450 m. Topography was dominated by an extensive central plateau and encircling higher relief mountains. The climate was characterized by long, cold winters and short, cool summers. Average study area precipitation was around 60 cm; above 2130 m most of this occurred as snow.

Most of the study area lay in the subalpine zone. Closed canopy forest covered approximately 75% of the landscape. Most of this forest consisted of lodgepole pine (Pinus contorta). Extensive contiguous nonforest areas occurred primarily below

2125 m. Occasional sizable nonforest enclaves occurred above 2275 m. Otherwise, nonforest areas occurred as rock and tundra above 3000 m or as smaller meadows in basins and on south- to east-facing slopes.

Large populations of ungulates, principally elk (Cervus elaphus) bison (Bison bison), moose (Alces alces), and mule deer (Odocoileus hemionus), shared the study area with grizzly bear. Other carnivores included, most notably, coyotes (Canis latrans) and black bear (Ursus americanus).

METHODS

Between 1974 and 1983, 2,561 aerial locations of radio-instrumented grizzly bears were made within Yellowstone National Park. By 1983 computer files of digitized habitat type (Mueggler and Stewart 1980, Steele et al. 1983) and cover type (Despain, in press) maps were available for Yellowstone Park; methodology had also been developed for deriving bear-specific coefficients of habitat value for habitat types and habitat type-cover type combinations (Mattson et al., in press). We used these data and conceptual developments, along with a 1.5 km interval grid map and digitized road and development data, for our analysis.

We conducted our analysis at two scales: one defined by a 0 to 1500 m, the other by a 0 to 15 km buffer along roads and around developments. Both scale buffers were divided into parallel and concentric zones 100 and 1000 m wide, respectively. The zone adjoining a road or development was again halved; a total of 16 zones in each buffer were thus created. These zones

were the basis for Chi-square and graphics analyses.

Correspondence of zonal bear location frequency distribution (observed) with zonal grid point frequency distribution, weighted by average habitat productivity score (HPSzk), (expected) was tested by the Chi-square statistic. Cells with fewer than five observations, to the point they comprised less than 20% of all cells, were either excluded from analysis or consolidated (Sokal and Rolf 1969). The analysis was stratified by season and type of primary human emplacement, either road or development (that is, village or front-country campground). Seasons were defined as spring (March 1 through May 31), summer (June 1 through August 31), and fall (September 1 through November 15).

Specific zonal bounds for Chi-square analysis resulted from an iterative process. Observed and expected frequency distributions were initially examined across all zones. Major sign consistent deviations of observed use from expected use were noted progressively outward from either roads or developments. The first sign break in a major pattern (that is, observed intersecting expected) was designated midpoint of the larger zone for which Chi-square analysis was conducted. In the absence of major patterns, all 16 zones were included in the analysis.

Zonal grid-point frequency was weighted by average zonal habitat productivity score (HPSzk) for conceptual reasons. Expected bear use did not logically result from proportionate area alone; habitat productivity necessarily played a major role. Derivation of habitat productivity scores for each season k was described by Mattson et al. (in press). Calculation of average zonal productivity scores and nonforest area was based on

proportionate habitat and cover type representation derived from intersection of circular 0.5 km radius scan areas with digitized map data. Grid points and bear locations served as foci for scan circles. Data management, calculation of distance to nearest road and development, and intersection of scan areas with map bases were accomplished by the Spatial Information System (SIS) software package (Hoskins 1984).

Figures were also constructed in which zonally averaged variable levels or variable frequencies were ranged against zone. These allowed visual inspection and biological interpretation of zone-specific variable distributions.

RESULTS

In results and discussion we have used three terms that describe tolerances of individual bears to human presence. We used the term "wary" to designate bears that characteristically flee from human encounters and avoid areas with human developments. The term "neutral" was applied to bears indifferent to human presence or developments, but not actively seeking human-related foods. Given reward, neutral bears are predisposed to become "habituated." The term "habituated" was applied, then, to bears tending to search out human-related foods (Haroldson and Mattson 1985). We have also employed phrases such as "road effects" and "development impacts," fully realizing that humans rather than physical structures precipitated impacts on bears.

Our analysis and results are reported at two different resolutions, hereafter called "micro" and "macro." The micro

scale (a 1-1500 m buffer) was more sensitive to adjustments made by more or less neutral bears residing within a zone of influence impinging on other more wary bears. The macro scale (0-15 km buffer) was more sensitive to population adjustments such as the displacement of less neutral bears to ranges further from primary human emplacements.

Zonal habitat productivity (HPSzk) varied considerably with distance from primary roads and developments and with season (Fig. 2). Spring habitat productivity was highest within 5 to 7 km and peaked within the first kilometer of primary human emplacements. Summer and fall zonal productivity was highest and peaked well away from roads and developments, generally beyond 8 km; fall productivity was markedly low within 6 km.

Primary roads and developments in Yellowstone National Park were squarely on top of the highest productivity spring bear habitat. This concurrence was understandable. Most roads and developments were along watercourses at comparably lower elevations. Such areas coincided with major ungulate winter ranges and habitats supporting spring-green vegetation, both major spring components of grizzly bear habitat in Yellowstone Park (Knight et al. 1984).

Representation of nonforest habitat strongly peaked adjacent to roads and developments, then dropped sharply to 2-3 km, leveled, and dropped again to 6 km (Fig. 3A). Bear use of nonforest habitat appears to have been disrupted during all seasons, but especially during spring and summer (Fig. 3B). During spring, compensatory increased use of nonforest habitat was not evident until beyond approximately 2.5 km. Similarly,

during summer, compensation consonant with the decline and high summer value of nonforest habitat (Knight et al. 1984) was not evident before approximately 2.5 km. Compensation during fall was not apparent until beyond 1.5 km.

Results of micro-scale chi-square and graphics analyses evidenced differences in bear response to roads and developments, by season. Roads appear to have been more impinging than developments (Fig. 4). During spring, depressed use out to 600 m along primary roads was evident. Frequency distribution of bear locations, including compensatory inflated levels beyond 600 m, significantly differed ($P < 0.005$) from that expected by area and habitat productivity. Summer bear locations evidenced a similar pattern. Although marginally significant in a statistical sense ($0.05 < P < 0.10$), we imputed biological significance to the summer pattern because of consistent depressed use out to 600 m and consistent inflated use beyond. No road effects were apparent on a micro-scale during fall.

Development centered micro-scale analysis results contrasted with those of roads (Fig. 5). Insufficient data precluded analysis of spring effects; substantial depression of bear use close to developments was not evident during summer and fall. Congruency of zonal levels of expected and bear use characterized summer (Fig. 5A). During fall (Fig. 5b), bear use tended to be inflated above that expected closer to developments. Differences in observed and expected fall use levels out to 1500 m were statistically marginally significant ($0.05 < P < 0.10$). Occupancy of the 1500-m zone around developments by neutral and

habituated bears during the study period is strongly suggested by these summer-fall results.

Results of macro-scale (0-15 km) chi-square and graphic analyses also suggested differences in bear response to roads and developments, by season. Macro-scale displacement, in contrast to the micro-scale, appears to have been greatest in the vicinity of developments. During spring (Fig. 6A), depression of use around developments was relatively minor. Observed use was substantially less than expected out to approximately 1.5 km. The pattern of observed deviated only marginally from expected out to 8 km ($0.05 < P < 0.10$).

During summer, development impacts were major ($P < 0.005$) but varied (Fig. 6B). Observed and expected frequency of bear use was congruent out to 2 km. Beyond 2 km to approximately 5.7 km, observed use was substantially less than that expected by area and habitat productivity. A second deviation of observed use below expected occurred around 8 to 9 km. Conversely, inflated use characterized the 6 to 7 and 10 to 11 km zones. The 0 to 2 km pattern suggests the presence of neutral and habituated bears, the 2 to 6 and 8 to 9 km deviations, displacement of more wary bears, and the inflated use around 6 to 7 and 10 to 11 km, compensatory adjustment. The double pattern of depressed and inflated use could be interpreted as evidence of two cohorts of bears differentiated by sensitivity to human presence and/or behaviorally induced within-species spacing.

Development effects were apparent during fall ($0.05 < P < 0.10$), but were less than those evidenced for summer (Fig. 6C). Marginally greater bear use than expected in the 0 to 1 km zone

corroborated micro-analysis results and the presence of habituated bears. Consistent but marginally depressed use was evidenced out to approximately 4.7 km. Compensatory inflated use occurred between 5 and 7 km. Although statistically marginally significant, we imputed biological significance to this pattern because of its consistency and interpretability.

Deviation of observed from expected levels of bear use in zones paralleling roads was highly significant ($P < 0.005$) during all seasons. During spring, substantial depression of use out to approximately 0.8 km corroborated micro-analysis results (Fig. 7A). Considerably inflated use between 0.8 and 2.5 km could have reflected several factors, most likely: (1) compensation for displacement; (2) under-valuation of habitat by HPSzk, arising from greater year-to-year consistency in availability of high value spring foods within this zone; (3) displacement of subadults to this zone by other more dominant bears; and (4) substantially increased cover beyond roughly 1.5 km. During summer (Fig. 7B), no displacement effect was evident except that already indicated by micro-analysis for the 0.0 to 0.6 km zone. Inflated bear use between 1 and 4.5 km is most logically tied to the disproportionate presence of subadults in this zone. As we will discuss later, this subadult presence was likely due to displacement by other more dominant bears rather than innate quality of habitat. Displacement was suggested during fall (Fig. 7C) for the 0 to 4 km zone; inflated use was apparent in the 4 to 7 km zone. Forest cover substantially increased at the 4 km transition and may explain some difference in use between the two zones, especially during this season when

use of whitebark pine (Pinus albicaulis) nuts in host forest habitat was so critical (Mattson et al., this volume).

We also investigated influence of primary human emplacements and associated human activity on zonal distribution of bear classes. Individual bears that contributed to our data base were classified as either fully mature adults (Ad), subadults (SAd), or older subadults - young adults (SAdAd). Average Ad ages at first and last years of tracking were 10.8 and 14.8, respectively. Respective ages for SAdAd were 4.1 and 9.1, and for SAd, 3.1 and 4.7. SAd's were typically tracked later and SAdAd's earlier in the study period. Thus, most individuals of the SAdAd class were young adults at the time data was collected on the SAd class. This classification accommodated individual bear tracking histories and also vulnerabilities to man-induced mortality.

During all seasons subadults were proportionately most abundant close to roads (Fig. 8). Representation of subadults diminished to near zero, typically between 10 and 15 km. We interpreted this trend to be the result primarily of subadult displacement by more dominant bears. This phenomenon has been documented for brown bear concentrated in high quality habitat (Hornocker 1962, Egbert and Stokes 1976). Observations and research in Yellowstone Park (Schleyer et al. 1984, Harting 1985) have also suggested that such a phenomenon is operative in more dispersed populations. Concentration of the subadult class along roads is therefore logically attributable in part to displacement effected primarily by more dominant young adult and fully adult bears established in more secluded habitat (see Table 1). A

similar but less clear-cut trend of greater SAd representation closer to developments was also apparent; diminishment of the SAdAd class was, however, a stronger trend in zones closer to villages and campgrounds.

Grizzly bear foraging efficiency was also impacted by primary human emplacements. In nearly all zones beyond the conceivable influence of roads and developments, grizzly bear occupied habitat substantially more productive than was average for the zone. This implies that, where allowed, bears actively selected more productive sites from amongst those available. However, productivity of habitats occupied by grizzlies was close to or depressed below the average in zones proximal to roads and developments during all seasons. By implication, grizzly bear foraging strategies directed towards habitat optimization were disrupted by the front-country human presence. This disruption extended out to approximately 3.5 km around developments during spring and summer; bears were less affected during fall (Fig. 9). Foraging was also disrupted along roads out to approximately 2.5 km during spring and summer and out to 4 km during fall (Fig. 10). These results logically tie to the previously noted disruption of compensation for zonally declining availability of nonforest habitat out to approximately 2.5 km during spring and summer and out to 4 km during fall.

Knight and Eberhardt (1984 and 1985) have suggested that the Yellowstone grizzly bear population is marginally viable; that loss of an additional one or two females per year could lead to eventual extinction. They have stated that adult reproductive females are key to the near future welfare of the Yellowstone

grizzly population. For these reasons, we conducted a secondary analysis specific to adult females ($n = 8$) during summer. Results were consonant with those already reported (Fig. 11), although effects on zone occupancy and foraging tended to be more pronounced.

From adult female specific results we calculated proportionate reduction of habitat effectiveness along roads and around developments due to reduced use (D_d and D_r) and disrupted foraging (D_{HQd} and D_{HQr}) within specified zones (zones of influence, ZI). We then calculated total reduction of habitat effectiveness within Yellowstone Park due to roads ($TDr(hq)$) and developments ($TDd(hq)$). Total effective loss of habitat ($TDdr(hq)$) was derived by addition of $TDr(hq)$ and $TDd(hq)$ after accounting for overlap of road and development zones of influence. Details of these calculations are in Appendix 1.

Calculation results indicate that 15.7% of available habitat production in Yellowstone Park was not used by adult females during summer because of primary road and development effects. This habitat loss was due to suboptimal utilization as well as outright avoidance. If an adult female population near 50 is assumed (Knight and Eberhardt 1984), additionally that near 30 of these animals resided predominantly within the park's boundaries, and that Yellowstone Park was near carrying capacity (Picton et al., in press), then this effect roughly translates into loss of habitat sufficient to have supported five or six adult females.

In a final analysis we investigated individual habitat occupancy and additive yearly probability of mortality with respect to developments. Individual bears ($n = 28$) fell into one

of three groups defined by modal zone proportionate relocation density. These three groups corresponded to bears with a peak relocation density between (1) 0 to 3 km, (2) 3 and 9 km, and (3) 9 and 15 km of developments. Bears characteristically using habitat closest (0-3 km) to developments were likely habituated and almost certainly neutral to predictable high density human presence.

Fully adult grizzlies (Ad) evidenced a distinct bimodal distribution across the three zones (Table 1). For both males and females, neutral/habituated bears characterized by modal occupancy of the 0-3 km zone were distinct from another, probably more wary, group occupying the 9-15 km zone. Males were more likely to be occupants of the closer zone than were females. Subadults (SAd) and young adults (SAAd) evidenced antithetical trends across the three zonal groupings. All six young adults were modal occupants of the 9-15 km zone; subadults were more often occupants of the 0-3 and 3-9 km zones.

Striking trends in probability of man-caused mortality were also apparent between bear classes and across zonal groups (Table 1). Adult occupants of the 0-3 km zone apparently stood twice the risk of mortality as similar occupants of the 9-15 km zone; however, risk was nearly five times as great for females and only marginally greater for fully adult males in the nearer of the two zones. Conversely, indicated probability of mortality among subadults increased further from developments. In the near vicinity of developments, fully adult females were apparently in greatest and subadults in least risk of man-caused mortality. This pattern was opposite to that indicated for the

9-15 km zone where mortality risk was, progressively, least to greatest in the Ad(F), Ad(M), SAdAd, and SAd classes.

A behavioral interpretation of these distribution and mortality risk patterns is most logical. Subadults were very likely displaced, as we have noted before, by fully adult and young adult bears. This was evidenced by two trends: (1) modal representation of subadults primarily in the two less secure zones nearer human habitation, and (2) highest probability of mortality amongst subadults co-occupying the 9-15 km zone with what were probably adult bears wary of the human presence. Thus, subadults were probably displaced across zones towards less secure habitat proximal to developments and, within the 9-15 km zone, towards population sinks.

High adult female mortality risk closest to developments was a consequence of habituation. This is corroborated by unpublished histories of individual bear management actions. Conversely, lower mortality risk for subadults and adult males modally distributed in the 0-3 km zone was probably a consequence of neutral rather than habituated behavior. This is again corroborated by individual bear histories and by intensive study of one of the subadults occupying the 0-3 km zone (Haroldson and Mattson 1985).

Markedly low subadult mortality in this zone can also be attributed to the nature of interaction with fully adult bears. Because most adult bears in the 0-3 km zone were likely neutral or habituated to human presence, the within-zone, between bear-class displacement of subadults to population sinks, evidenced in the 9-15 km zone, was not likely. Therefore,

subadults were likely occupying productive natural habitat and evidencing neutral behavior within the 0-3 km zone while especially adult females were focusing on human-related foods. This is corroborated by average habitat productivity scores (HPSzk) for the different bear classes; subadults consistently occupied productive natural habitat in the 0-3 km zone.

DISCUSSION AND CONCLUSIONS

Simple interpretation of results was complicated by biases inherent in aerial location of radio-instrumented bears. Most locations occurred in the morning hours. Because of grizzly bear diel activity patterns in the Yellowstone area (Schleyer 1983, Harting 1985), the likelihood was high that habitat use conducted under cover of darkness went undetected. This problem was especially likely for summer; nocturnal activity levels were highest during this season (Schleyer 1983).

The actual depression of use near roads and developments and complementary inflation of occupancy beyond very likely did not correlate with the proportionate difference between observed and expected use. Bears were probably making additional use of "zones of influence" under cover of darkness and evacuating during diurnal periods to more secure nearby habitat. Nonetheless, this does not discredit the fact that primary roads and developments were depressing or complicating grizzly bear use of habitat. For these reasons our calculated loss of habitat and concomitant five or six adult females could be revised down to three or four animals.

Another factor that complicated interpretation of observed/expected frequency distributions was the mortality effect associated with developments. Some macro-scale depression of observed relocation frequency below expected could be attributed to the higher mortality rate sustained especially by females in zones closer to developments. However, this effect was likely buffered by the low mortality rate amongst subadults

and moderate mortality rate amongst adult males in proximal zones and also by the probable attractant effect of villages and campgrounds on habituated and neutral bears.

A third major source of bias in our data was the suspected higher capture rate of habituated/neutral bears. This would have tended to proportionately increase relocations closer to roads and developments and, thus, mask some displacement effects. This bias would have further tended to counteract suspected macro-scale effects of higher mortality rate among habituated bears.

Assessment of our data corroborates the likely effects of differential capture and mortality rates on observed zonal frequencies. Consistent substantial negative deviation of observed from expected bear location frequencies was evident beyond 11 to 13 km around developments and 9 to 11 km along roads. We also calculated an index which quantified the probable effects of mortality on relocation data collected for a given zone (for details of calculation see Appendix 2); the greatest effects were calculated for the zones 9 through 15 km. It is likely, therefore, that a break in differential mortality and capture rate effects on relocation occurred at, roughly, 11 km. All our Chi-square and graphics analyses were, by our interative investigation, constrained to less than 11 or 12 km. We therefore concluded that these potential biases had little effect on our analysis.

We have shown that human activities attending primary roads and developments affected grizzly bears in Yellowstone Park in several ways. Occupancy of proximal habitat was reduced

concurrent with suboptimal utilization resulting from disruption of otherwise efficient foraging strategies. Subadults were displaced by other bears to less secure habitat adjoining developments. The 0-3 km zone surrounding developments was also an area of extremely high mortality risk to occupant habituated adult females. (Knight et al., in prep., will further describe the critical effects of human activities, including those associated with developments, as population sinks.)

Human activity associated with roads and developments had different effects on grizzly behavior during the study period. Roads tended to reduce proximal use on a micro-scale; developments didn't. In fact, micro-scale use proximal to developments was likely inflated during fall. This followed from association of habituated bears with human-related feeding opportunities present at developments but typically absent along roads. On the macro-scale, concentrated human activity at developments had a much greater effect on grizzly bear occupancy and utilization of habitat than did roads. This probably resulted not only from greater human density at developments but also, perhaps more importantly, from persistent high levels of human activity into nocturnal hours and excursions by humans during other times of day into adjoining habitat.

Substantial reduction of habitat effectiveness adjoining primary roads and developments has been demonstrated; however, this does not automatically imply negative consequences for the Yellowstone grizzly bear population. Virtually all mortality known for radio-instrumented bears has occurred at the hands of humans (Knight et al. 1985). Displacement may help create a

buffer between wary bears and human activities and refuse. This may, in turn, lessen exposure of these bears to human-related mortality risk.

However, sanitation of human developments is critical to preventing habituation of bears (Herrero 1985). Without sanitation, as the history of bear management in Yellowstone Park has shown (Meather and Phillips 1980), habituated behavior will develop in bears despite displacement effects. Displacement probably constitutes a measure of resistance to this behavioral degradation of survivorship.

Habituation was, by our assessment, apparently a critical factor in the demographics and survivorship of fully adult females. Habituated adult females that focused their activities around developments stood a strong probability of death within 4 years. For this reason, 8% of the park area was essentially unavailable to adult females and comprised the geographic extent of population sinks centered on developments during the study period. For the wariest adult females an additional 26%, or total 34%, of the park was not sufficiently secured from human intrusion. It is also notable that for those warier adult females tending to range more than 9 km from developments, survival for up to 20 reproductive years was likely. Thus, sanitation of developments is indicated to be the measure by which neutral adult females could occupy habitat near developments and yet not incur unacceptable risk of mortality associated with habituation.

Despite the potential beneficence of a displacement buffer, mitigation is warranted during some seasons. Very little

man-caused grizzly bear mortality has historically occurred in the Yellowstone area prior to July (unpubl. data). Thus, reduction of mortality risk by displacement is probably of no great consequence during spring. Habitat productivity is also concentrated during this season in the proximity of primary roads and developments. Mitigation is therefore recommended for spring, most logically by limiting motorized traffic during April and May on roads that transect prime ungulate winter range. Certainly, increased levels and duration of motorized traffic during these 2 months is not recommended.

Our documentation and quantification of displacement is also crucial to evaluating habitat effectiveness and thus carrying capacity in the face of permanent human emplacements. An analysis procedure (hereafter the C.E.A.) has been developed for the greater Yellowstone area (Weaver et al., in press) in which loss of habitat effectiveness due to human activity was modeled. Zones of influence and displacement coefficients were estimated for different human activities by a team of wildlife professionals familiar with grizzly bear behavior and displacement effects on other wildlife species. We compared displacement coefficients and zones of influence derived for primary roads and developments from our analysis with those estimated by Weaver et al. (in press). Arbitrary zones of influence estimated for the C.E.A. were less than zones suggested by our analysis. However, displacement was estimated by the C.E.A. team to be higher within the narrower zones. After adjusting for comparable zones of influence, the displacement coefficient, averaged over cover and noncover around

developments, estimated for the C.E.A. (0.320) came remarkably close to our derived coefficient (0.395). Coefficients for road effects were in the same ball park, but differed more substantially (C.E.A. = 0.175; this analysis = 0.307). In general, our analysis substantiated the intuition of knowledgeable professionals attempting objectivity.

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Table 1. Proportionate representation and additive yearly probability of man-caused mortality by bear-class and three zones of distance from developments. Zones correspond to 3 groups of peak habitat distribution for individual bears ($n = 28$).

BEAR CLASS	n	ZONES					
		0-3 km		3-9 km		9-15 km	
		PROP. OF TOTAL	PROB. OF MORT.	PROP. OF TOTAL	PROB. OF MORT.	PROP. OF TOTAL	PROB. OF MORT.
Ad	14	.428	.116	.143	.091	.428	.056
Ad(F)	8	.375	.256	.125	*	.500	.043
Ad(M)	6	.500	.101	.167	*	.333	.077
SAdAd	6	.000		.000		1.000	.108
SAd	8	.375	.000	.375	.145	.286	.250

* : sample size of 1.

Captions.

Figure 2. ~~sketch of productivity~~ ^{grizzly bear} Average habitat productivity score ~~road and development~~ (HPS_{ik}) for \checkmark macro-scale buffer zones ~~road and development~~, by season.

Figure 3. Percent nonforest area ~~and grizzly nonforest habitat~~ ~~use adjustment $(B_{ik} - G_i / G_i)$~~ for road and development macro-scale buffer zones; grizzly bear nonforest habitat use adjustment $(B_{ik} - G_i / G_i)$ for road buffer zones; where B_{ik} = average percent nonforest area associated with bear ^{relocation} scan circles in zone i for season k , and G_i = average percent nonforest area associated with grid points in zone i .

Figure 4. ~~Micro-scale~~ ^{relocations} observed (bear) and expected (grid ^{points} weighted by average HPS_{ik}) ~~test~~ frequencies and Chi-square analysis results, by season, for road buffer zones.

Figure 5. ^{relocations} Micro-scale observed (bear) and expected (grid points weighted by average HPS_{ik}) frequencies and Chi-square analysis results, by season, for development buffer zones.

Figure 6. Macro-scale observed (bear relocations) and expected (grid points weighted by average HPS_{ik}) frequencies and Chi-square analysis results, by season, for development buffer zones.

Figure 7. Macro-scale observed (bear relocations) and expected (grid points weighted by average HPS_{ik}) frequencies and Chi-square analysis results, by season, for development buffer zones.

Figure 8. Proportional representation of ~~subadult~~ subadult relocations in macro-scale road and development buffer zones and of young adults in macro-scale development buffer zones.

Figure 9. Average habitat productivity score (HPS_{ik}) for bear relocation and grid point scan ~~areas~~ areas, by season, for development buffer zones.

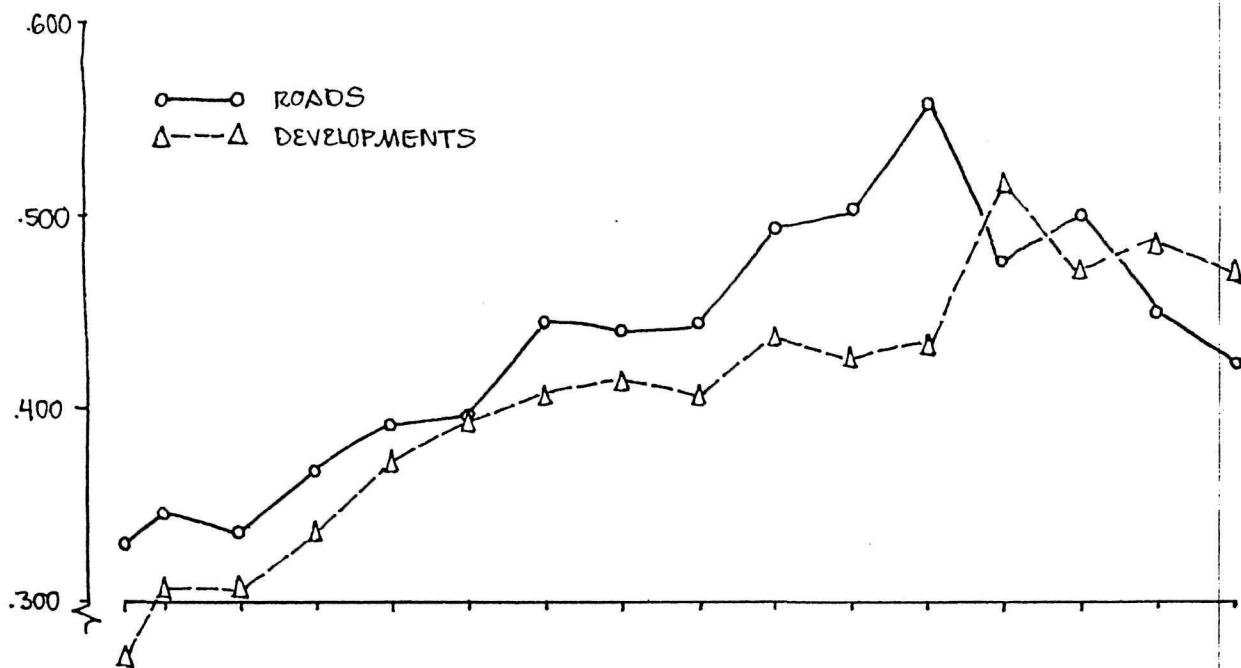
Figure 10. Average habitat productivity score (HPS_{ik}) for bear relocation and grid point scan areas, by season, for road buffer zones.

Figure 11. Macroscale observed (bear relocations) and expected (grid points weighted by average HPS_{ik}) frequencies and Chi-square analysis results ~~for adult females for summer~~ in ~~road and development buffer zones~~ and average habitat productivity score (HPS_{ik}) for bear relocation and grid point scan areas for adult females, for summer, in road and development buffer zones.

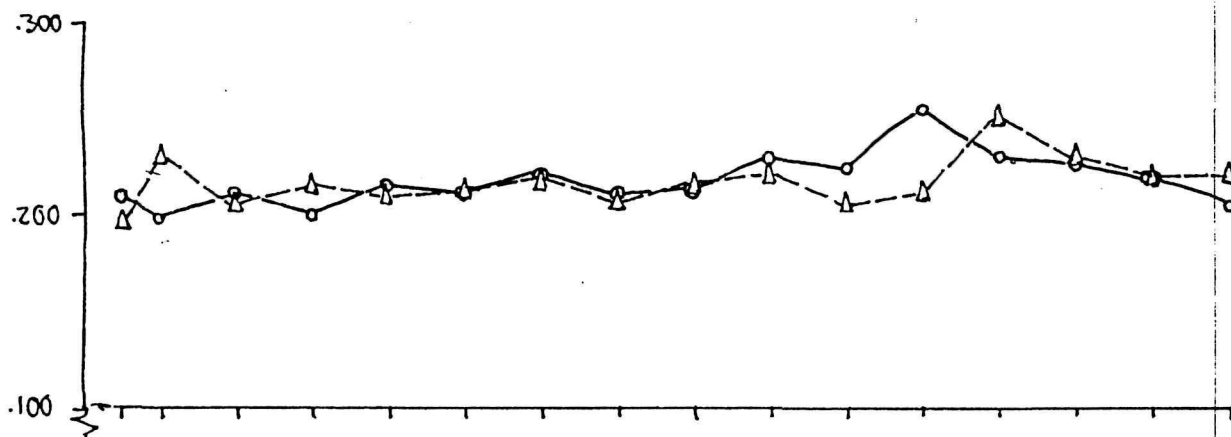
Figure 12. Average habitat productivity score (HPSik) for adult female, adult male, and subadult relocations during summer for development buffer zones.

HABITAT PRODUCTIVITY SCORE (HPS₂₄)

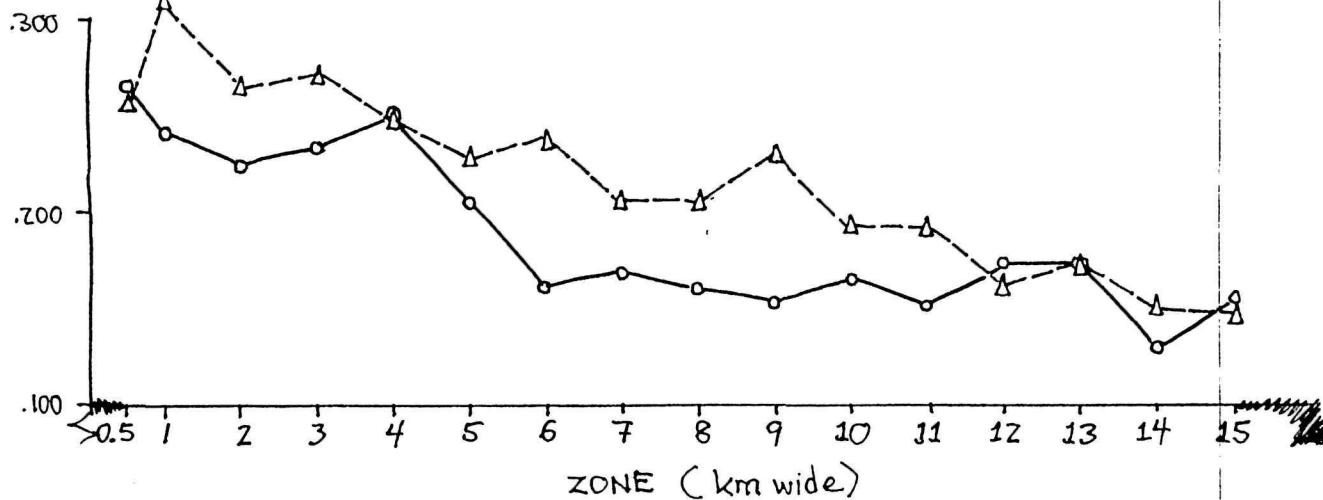
FALL

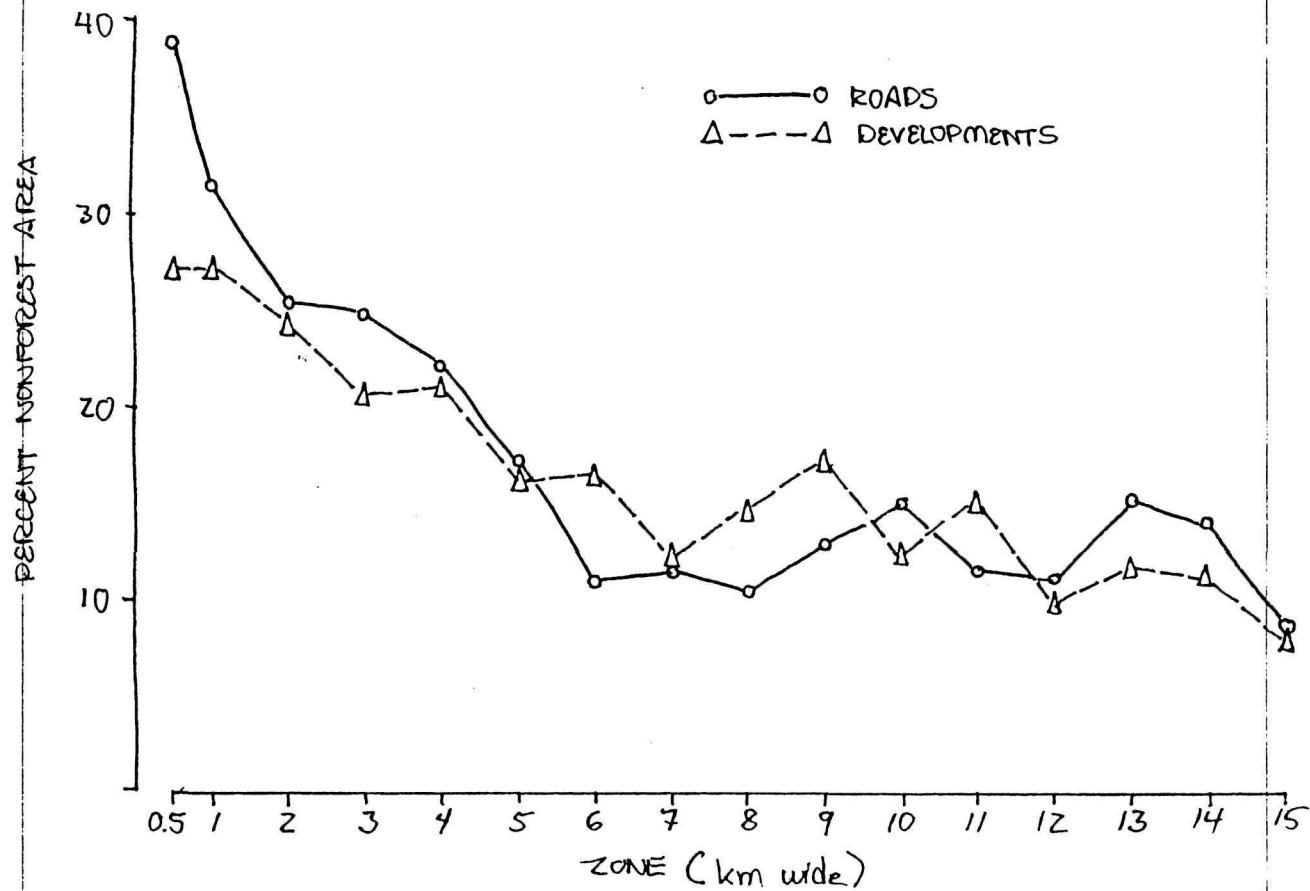
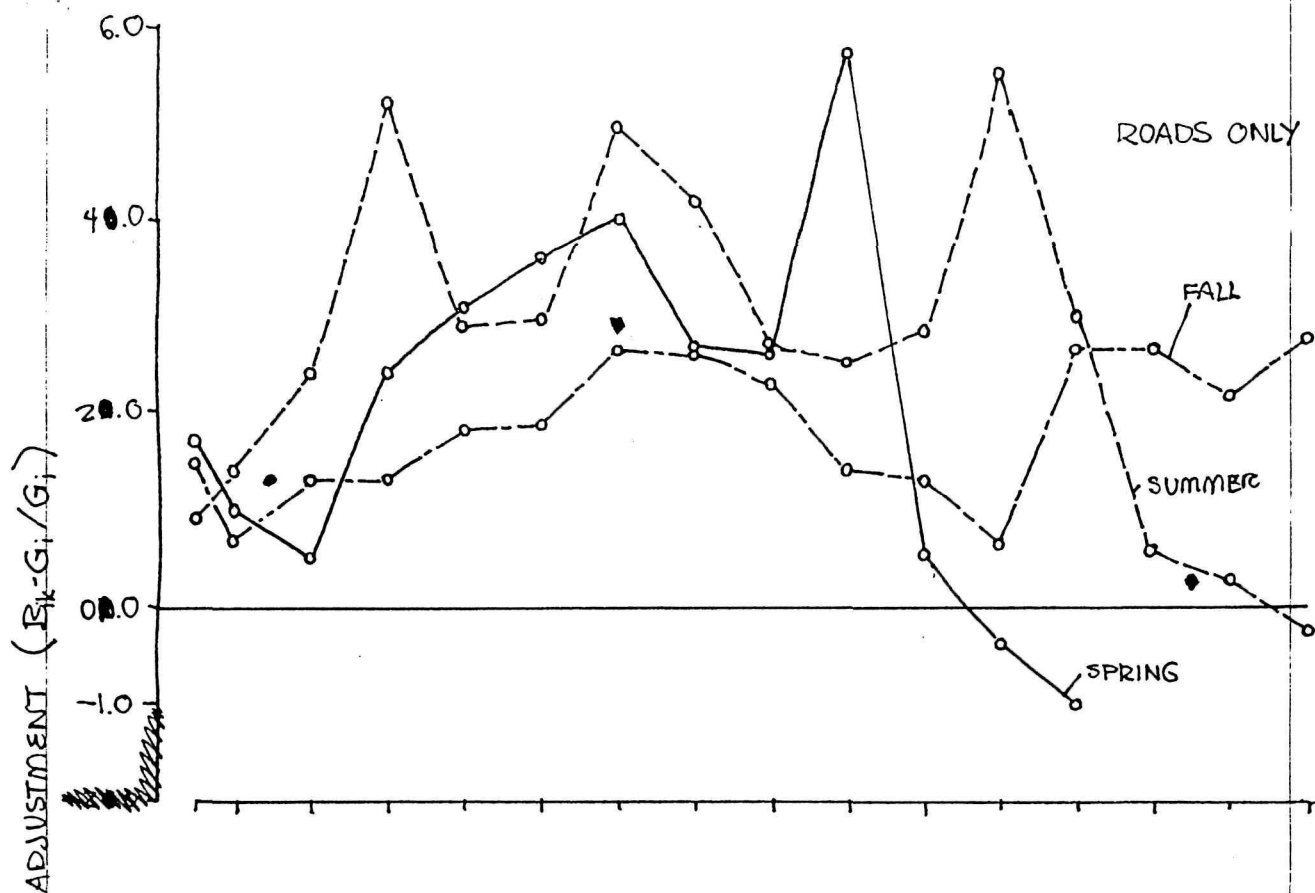


SUMMER

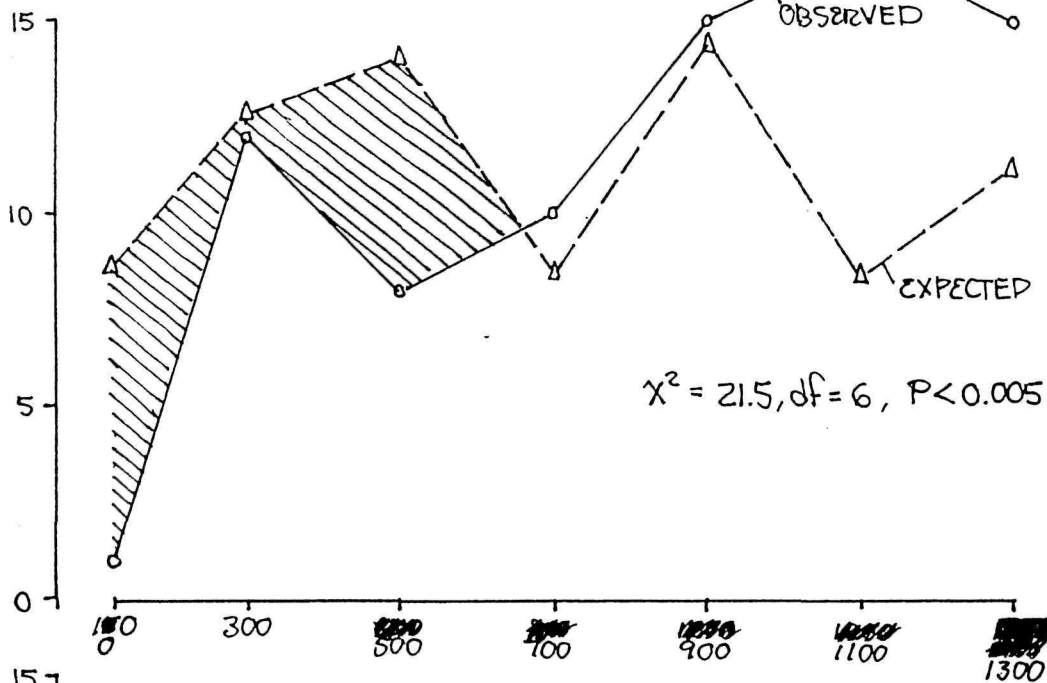


SPRING

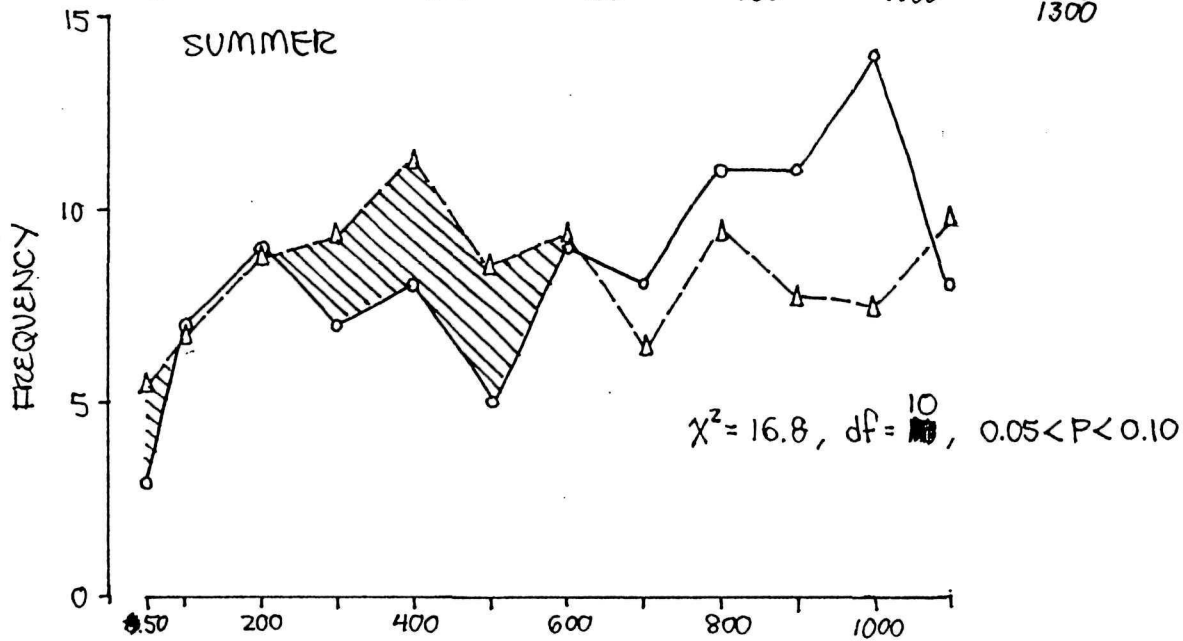




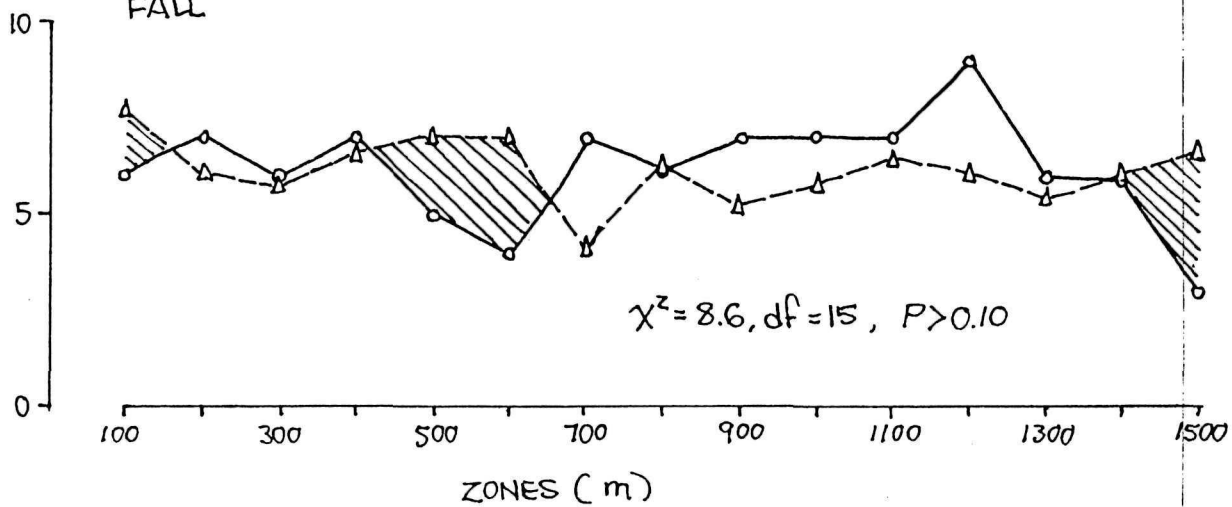
SPRING



SUMMER



FALL



ZONES (m)

(roads-micro)

Figure 5.

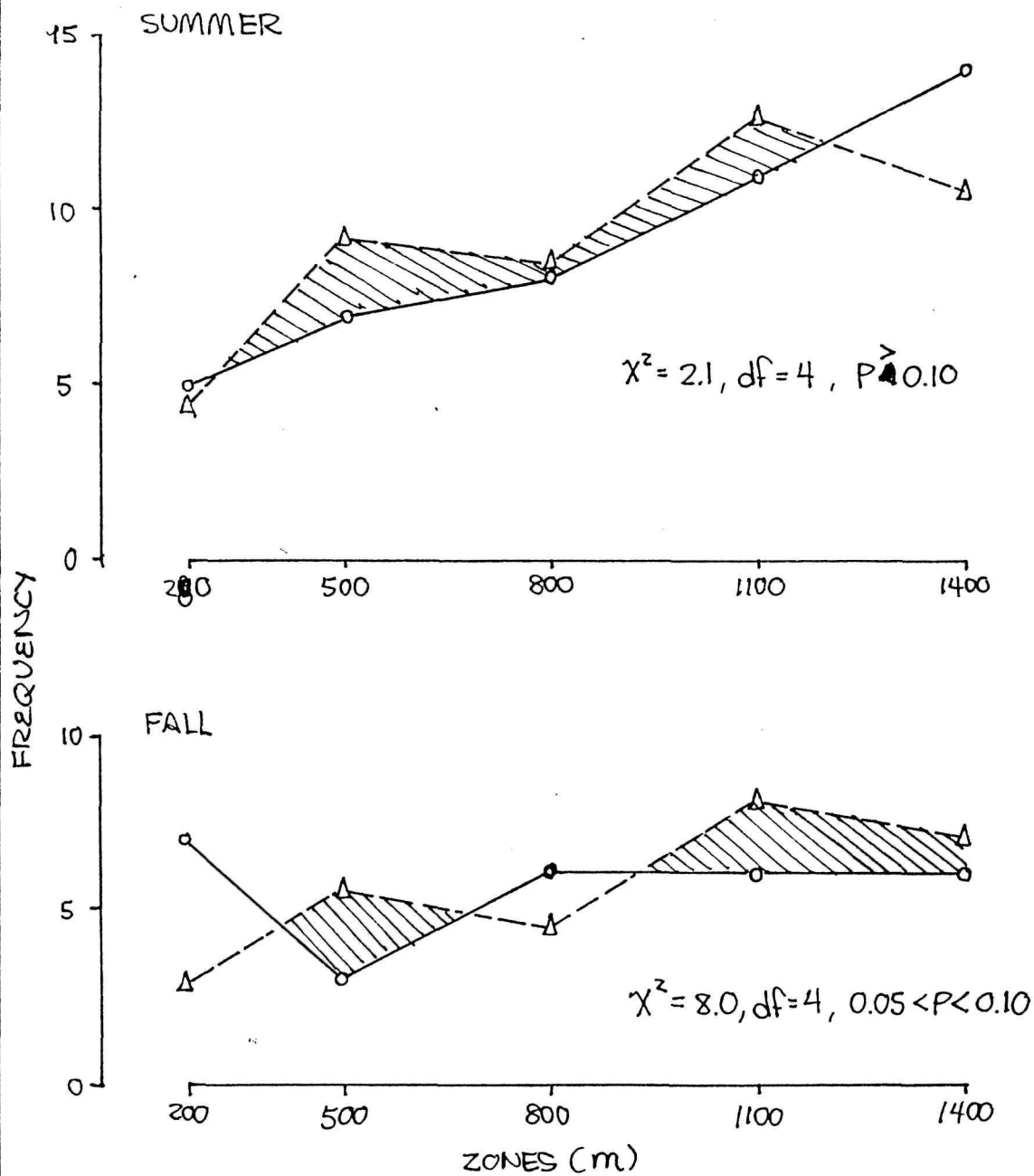
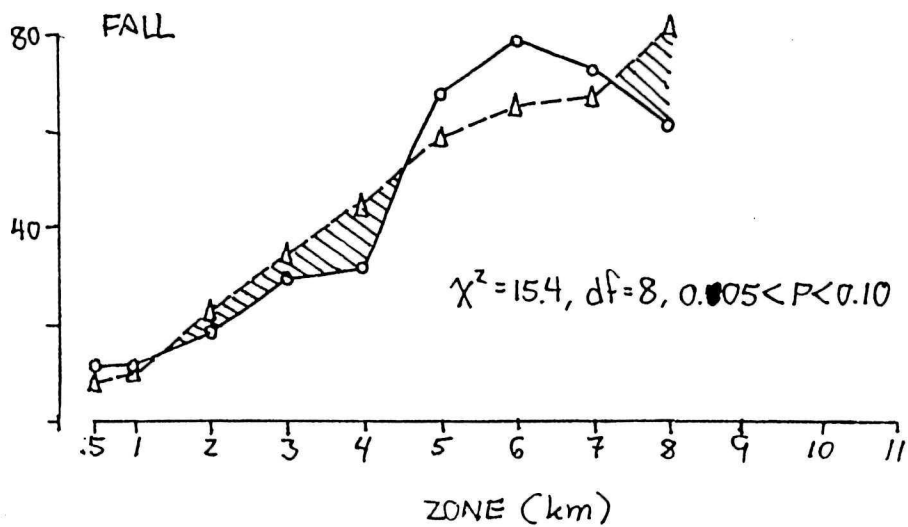
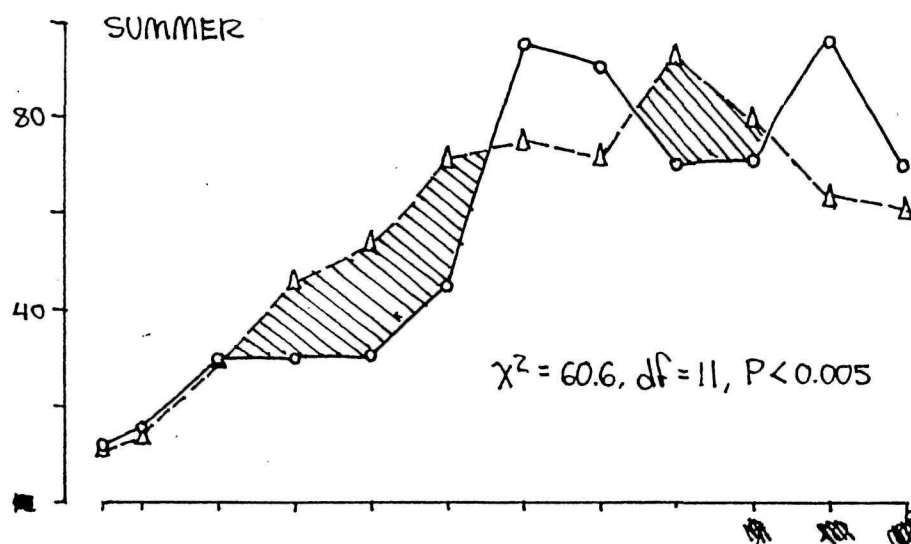
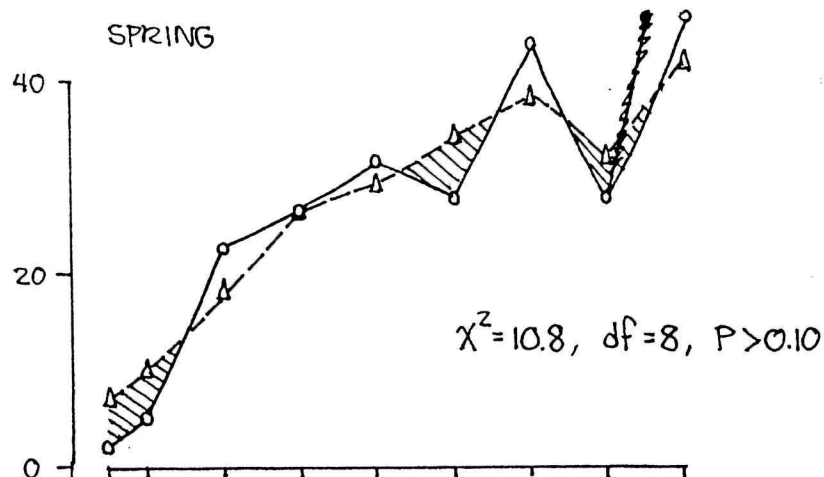


Figure 6.

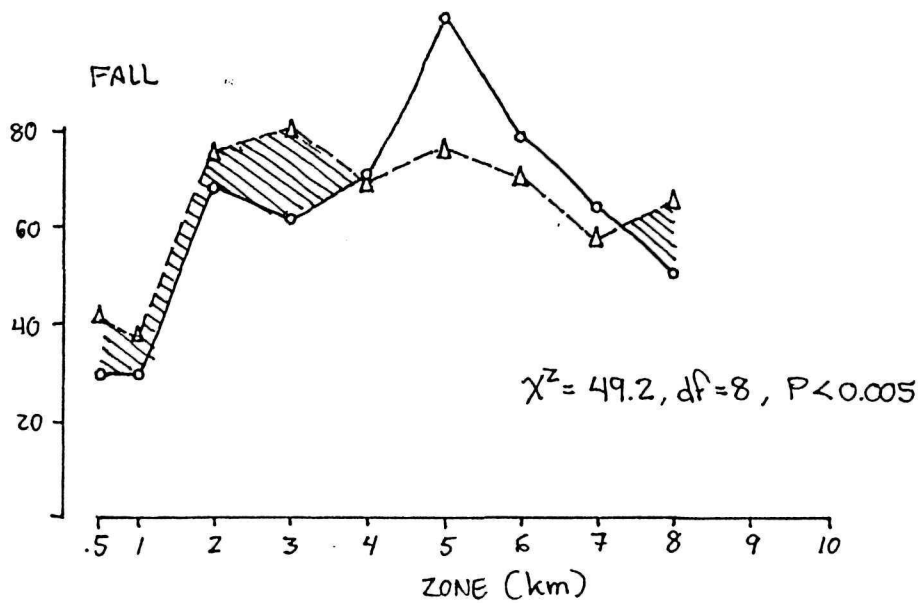
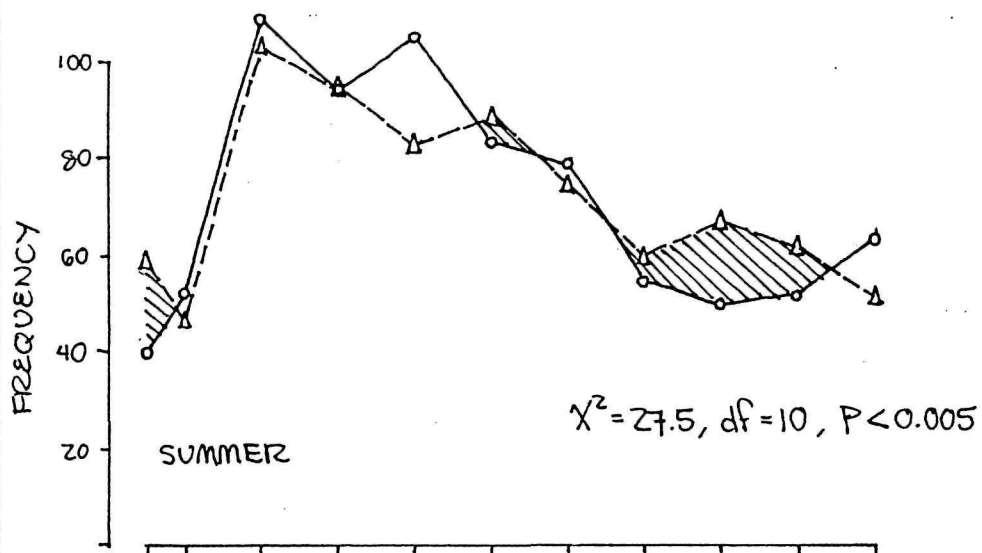
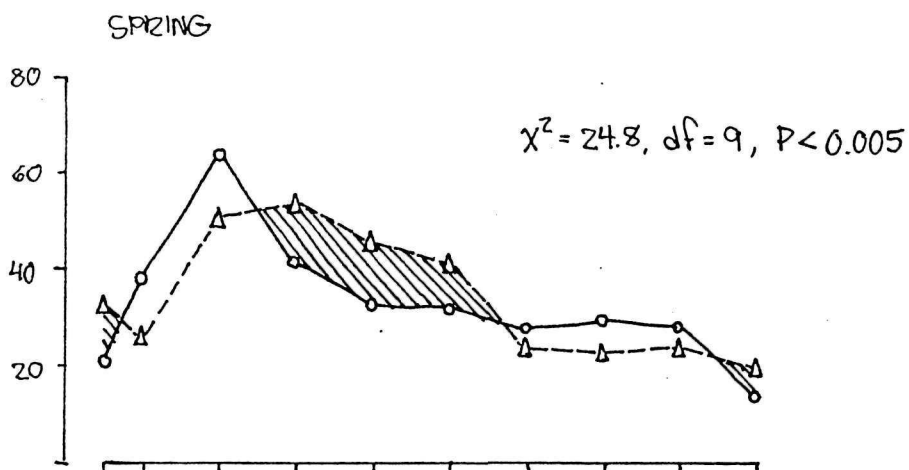


FREQUENCY

(macro-developments)

ZONE (km)

Figure 7.



(macro-reads)

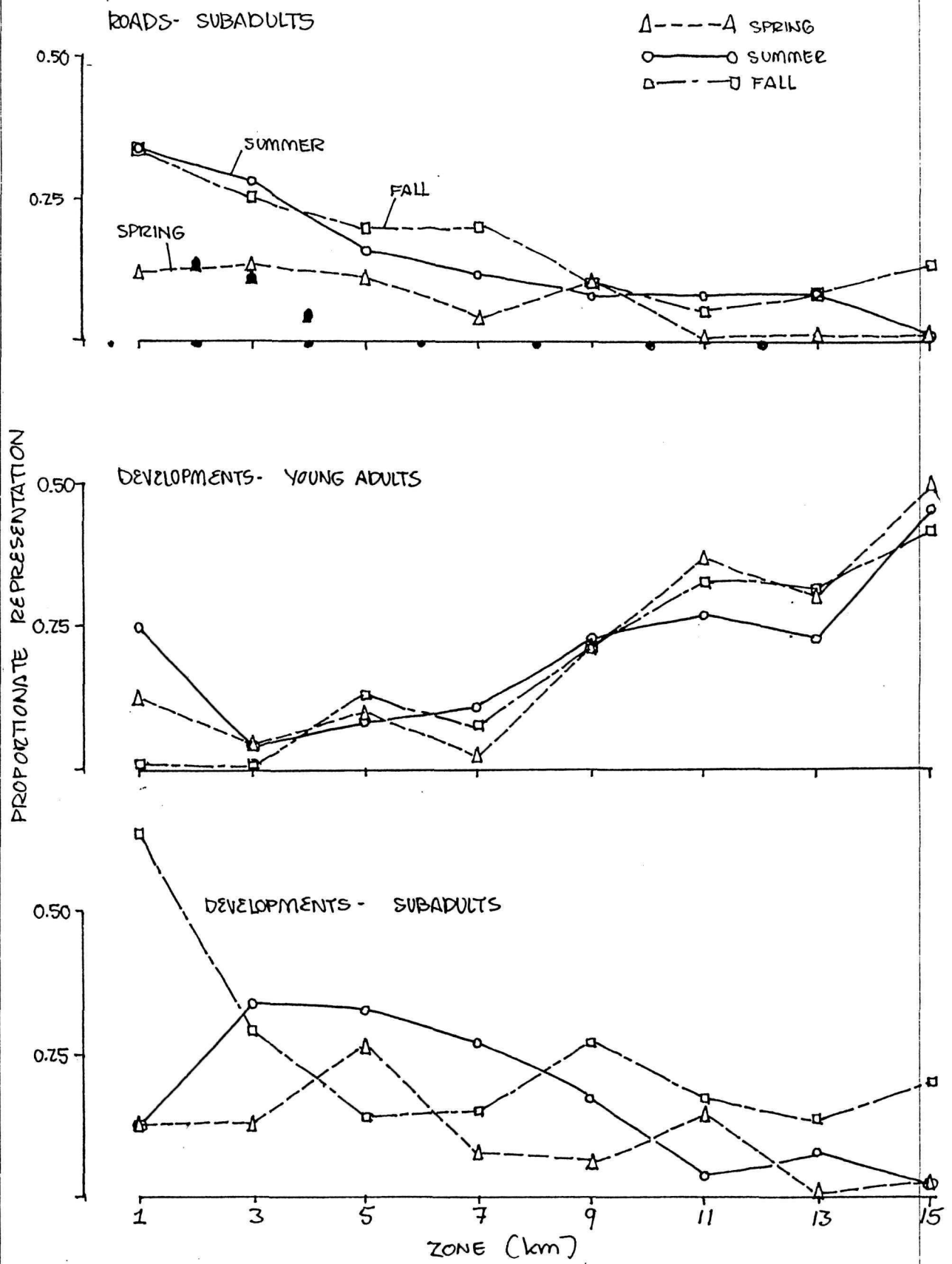
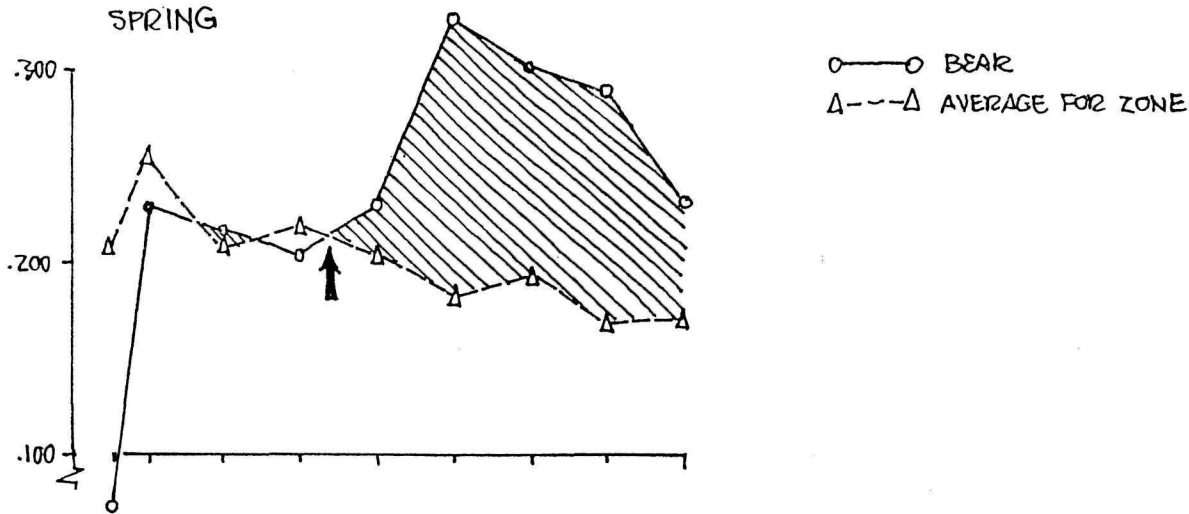


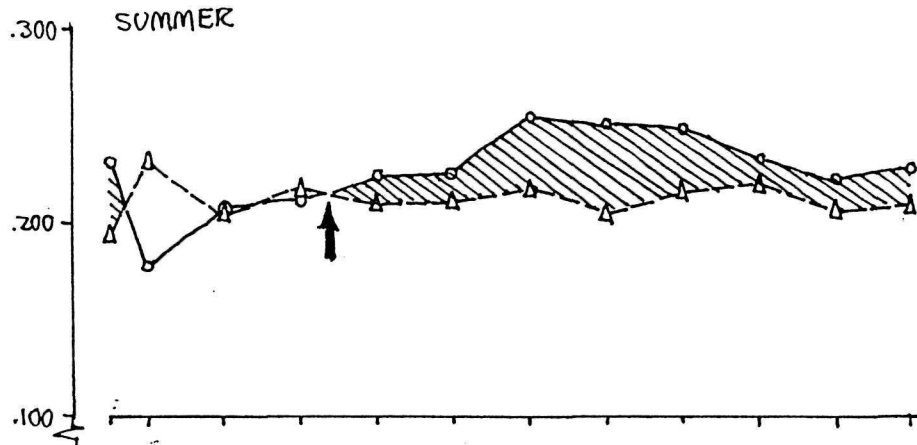
Figure 8.

Figure 4.

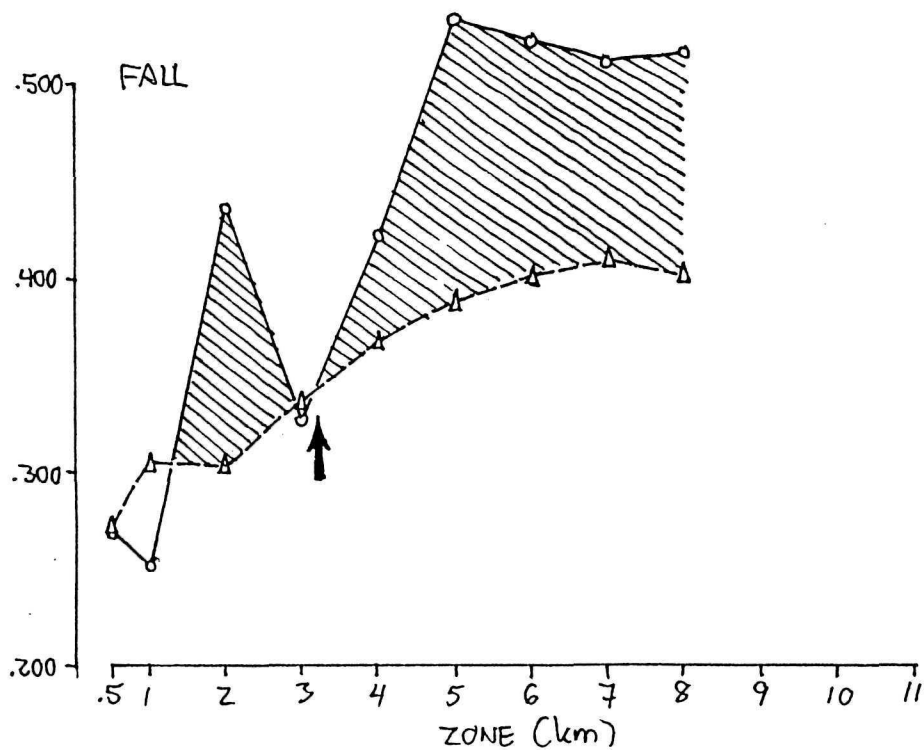
SPRING



SUMMER



FALL



HABITAT PRODUCTIVITY SCORE (HPS_{ijk})

development

ZONE (km)

ROADS

Figure 10.

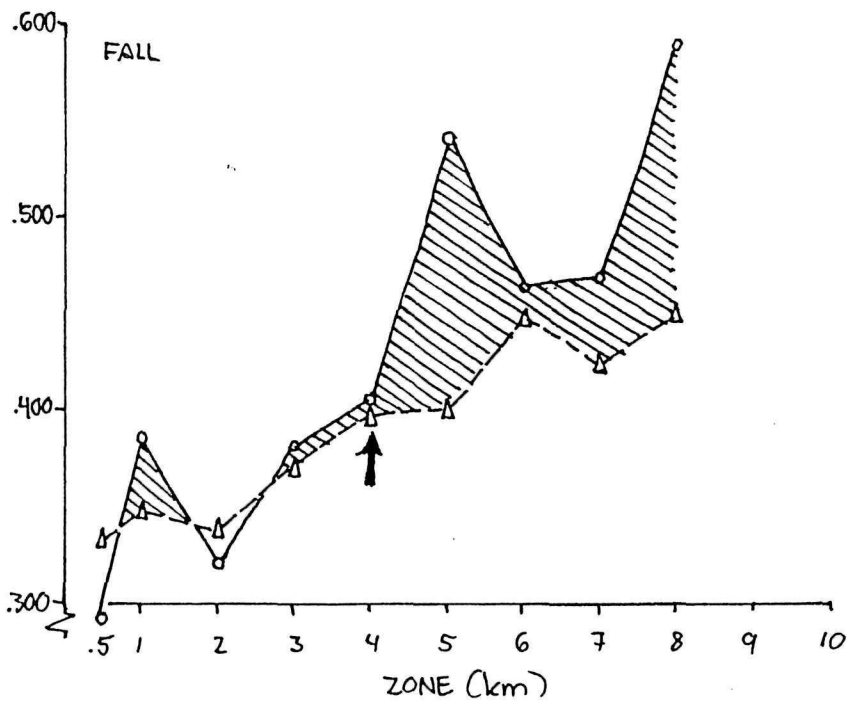
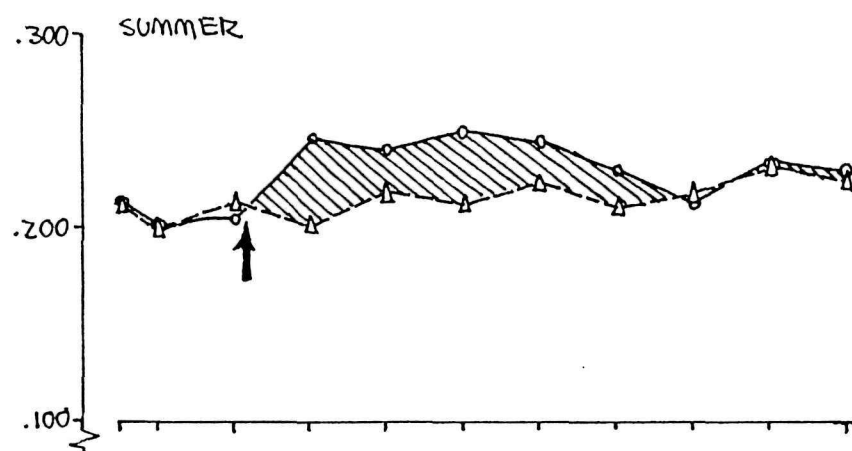
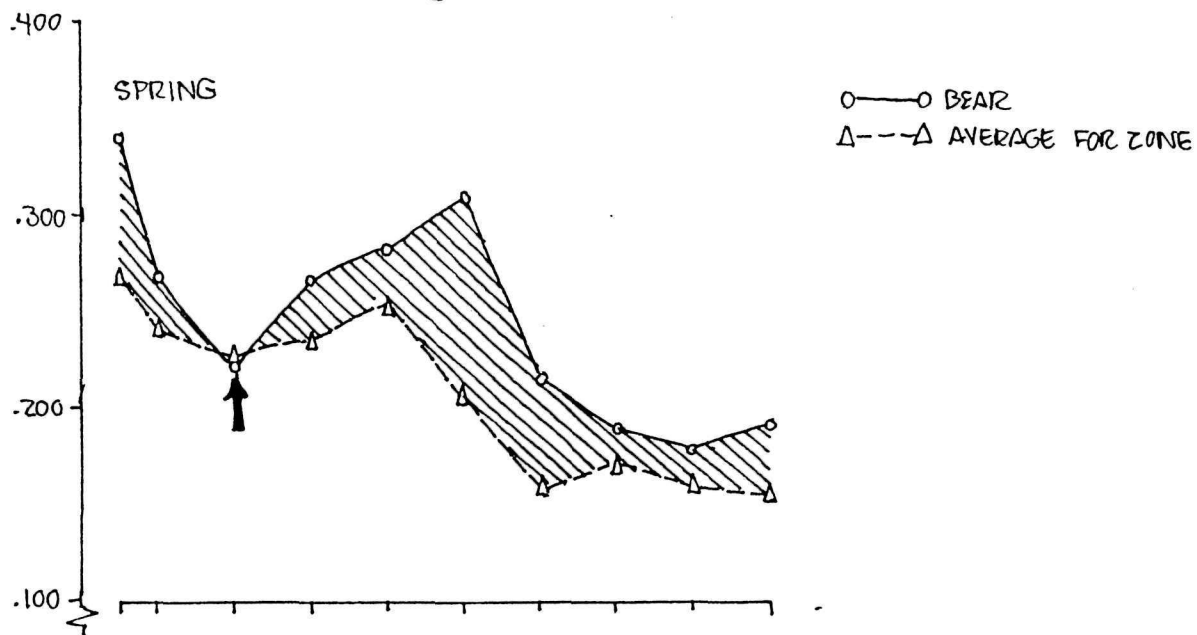
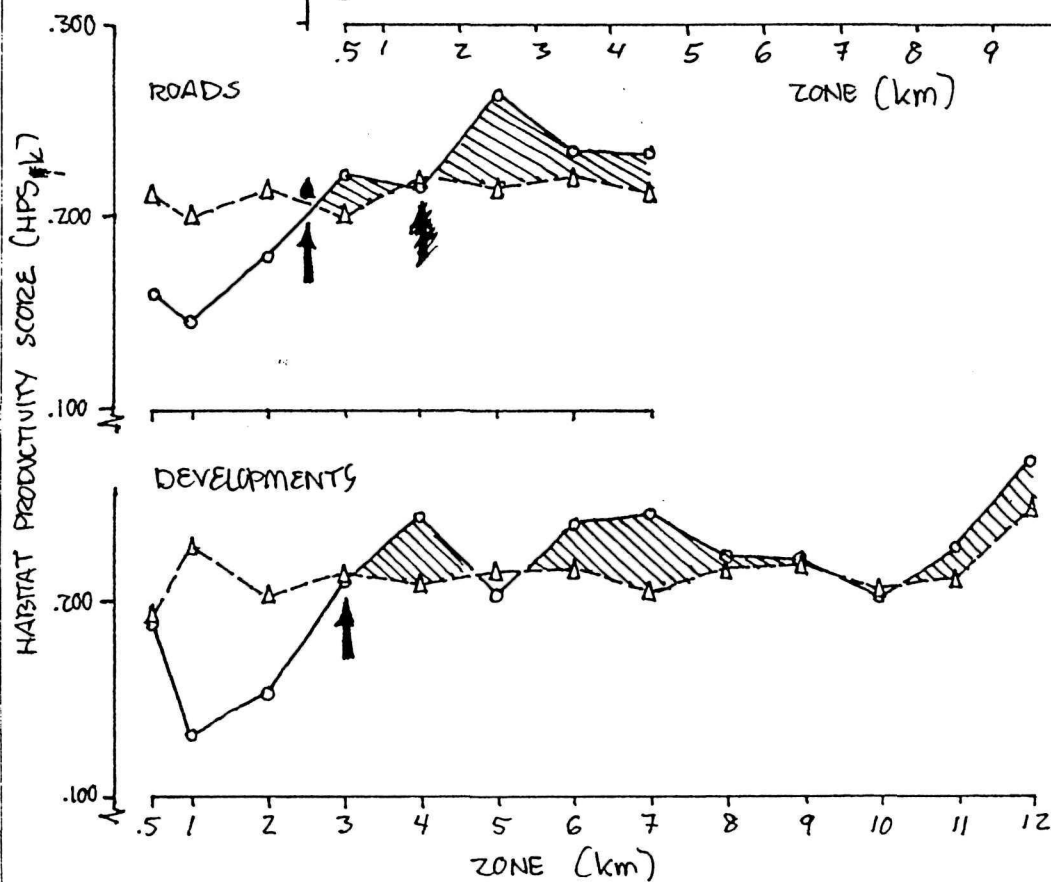
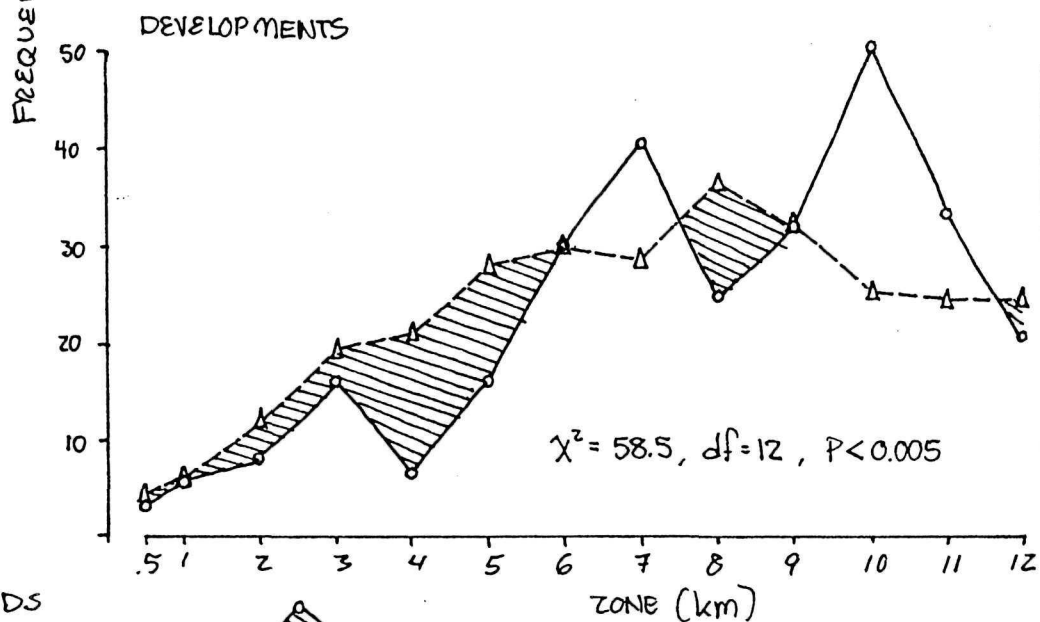
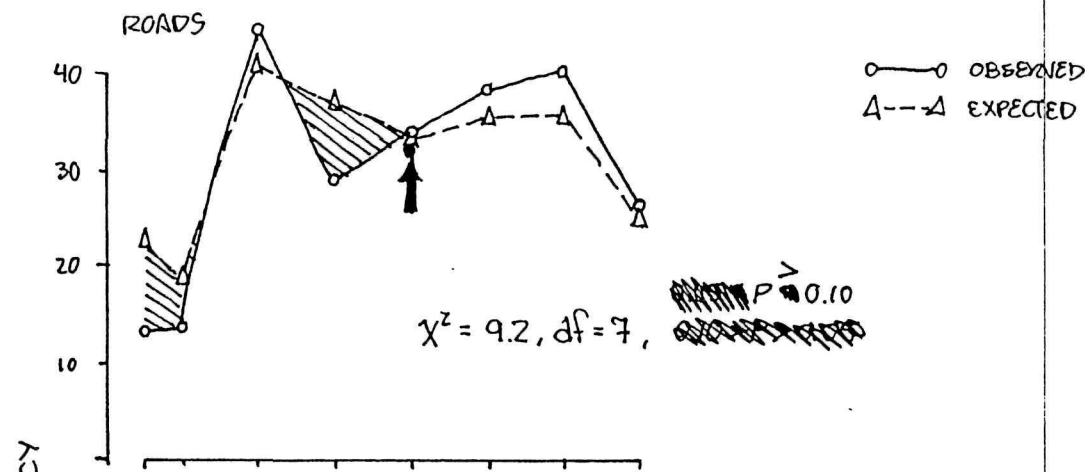
HABITAT PRODUCTIVITY SCORE (HPS_{1/2})

Figure 11. Adult ♀



APPENDIX 1.

E_{rik} : expected bear relocation frequency in zone i for season k in ~~section~~ in road buffer zones (E_{dik} for development buffer zones).

O_{rik} : observed bear relocation frequency in zone i for season k , in road buffer zones (O_{dik} for development buffer zones).

D_{zk} : displacement coefficient for influence zone z for season k , with respect to roads (D_{dzk} , with respect to development).

P_{rz} : proportion of total park area within influence zone z (P_{dz} , with respect to developments).

TD_{zk} : total displacement for zone z during season k .

AHQ_{rik} : ~~average grid~~ ^{average grid} ~~HPS_{ik}~~ ^{HPS_{ik}} for zone i during season k in road buffer zones outside displacement effect (EHQ_{dik} for development buffer zones).

OHQ_{rik} : observed HPS_{ik} for zone i during season k in road buffer zones outside displacement effect (OHQ_{dik} for development buffer zones).

ADJ_{rk} : adjustment factor for AHQ_{rik} ^{for season k} in road buffer roads within displacement effect (ADJ_{dk} for development buffer zones).

DHQ_{rzk} : ~~depression~~ ^{depression} coefficient for influence zone z during season k , with respect to roads (DHQ_{dzk} , with respect to developments).

DC_{rzk} : displacement/depression coefficient for influence zone z during season k , with respect to roads (DC_{dzk} , with respect to developments).

$TD(hq)_{rzk}$: total displacement/depression for influence zone z during season k , with respect to roads ($TD(hq)_{dzk}$, with respect to developments).

OLP : ~~proportionate~~ ^{proportionate} overlap between road and development and zones of influence

$TD(hq)_{r+d_{zk}}$ = total displacement/depression for influence zone z during season k due to roads and developments

$$Dr_{zk} = (\sum (E_{rik} - O_{rik})^+) / \sum E_{rik} \quad - \text{for negative sums only, within influence zone } z$$

$$TD^r_{zk} = Dr_{zk} * Pr_z$$

$$ADJ_{rk} = 1 + ((\sum (OHQ_{rik} - AHQ_{rik})) / \sum AHQ_{rik}) \quad - \text{for road buffer zones outside displacement effect}$$

$$DHQ_{rzk} = \sum ((ADJ_{rk} * AHQ_{rik}) - OHQ_{rik}) / \sum (ADJ_{rk} * AHQ_{rik}) \quad - \text{for road buffer zones within displacement effect}$$

$$DCr_{zk} = DHQ_{rzk} (1 - Dr_{zk}) + Dr_{zk}$$

$$TD(hq)_{rzk} = DCr_{zk} * Pr_z$$

$$TD(hq)_{r+d_{zk}} = (1 - OLP) TD(hq)_{rzk} + TD(hq)_{d_{zk}}$$

APPENDIX 2.

ZP_{ij} : density of proportionate relocations for bear i in zone j

FQ_{ij} : frequency of relocations for bear i in zone j

G_j : number of grid points in zone j

TZP_j : ~~sum~~ sum of ZP_{ij} across all bears in zone j .

IPM_i : ~~yearly~~ ^{additive} yearly probability of mortality for bear i , recorded as a mortality during the study period

YR_i : number of years bear i contributed to relocation data base

ZMS_j : zone mortality score, derived for all bears, i , recorded as a mortality during the study period

YR_i^* : number of years of history for bear i

ZSS_j : zone survival score, derived for all bears, i , known to have survived the study period

$ATZP_j$: adjusted sum of ZP_{ij} across all bears known to have survived the study period, in zone j .

MP_j : proportion ~~zone occupancy~~ zone occupancy attribute to bears recorded as a mortality during the study period.

MEI_j : ~~index~~ ^{probable} index of mortality effects on relocation data collected for zone j .

$$ZP_{ij} = (FQ_{ij} / FQ_{iTOTAL}) / G_j$$

$$TZP_j = \sum ZP_{ij}$$

$$IPM_i = 1 / YR_i^*$$

$$ZMS_j = \sum (IPM_i * ZP_{ij})$$

$$ZSS_j = \sum (YR_i * ZP_{ij})$$

$$ATZP_j = ZSS_j * (\sum ZP_{ij} / \sum (YR_i * ZP_{ij})) - \text{for bears known to survive}$$

$$MP_j = TZP_j^* / (TZP_j^* + ATZP_j) \quad - * : \text{for bears recorded as mortalities}$$

$$MEI_j = ZMS_j * MP_j$$