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Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada

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Abstract

Few studies have reported the effects of multiple human activities on grizzly bears, *Ursus arctos*. We document the degree of grizzly bear response to various human developments as a function of multiple interacting variables based on observed median distances to roads, trails and development features in a landscape where human presence is widespread. Female grizzly bears remained further than males from paved roads regardless of habitat quality or time of day. Males were found closer to paved roads when within or adjacent to high quality habitat and during the period of least human activity. The combination of traffic volume and highway configuration, however, overrides a bear's attraction to high quality habitats for high-speed, high-volume, highways. Avoidance of busy transportation corridors was strongest in the adult segment of the population. Bears were found closer to trails during the human inactive period when within high quality habitat and further from trails when distant to high quality habitat. Our data indicated an inverse relationship between the sexes in response to vehicles and traffic noise compared to the response to human settlement and encountering people. Female bears were found further away than males in relation to vehicles and traffic noise, yet found closer than males to human settlement and places where people may be encountered. Those males that were more willing to exploit high quality habitat near roads, did so at night and where hiding cover was present. Adult females were the most risk-averse cohort, choosing to avoid humans instead of seeking out high quality habitats. Adult female grizzly bears were influenced most by human activities and development. Management agencies must maintain access to high quality habitat, especially for adult females, and create new opportunities to support the reproductive potential of the population.

Keywords: Development; Grizzly bear; Human impacts; Response; Roads

1. Introduction

Many wildlife populations have been reduced to small fractions of their former size during modern times due to anthropogenic pressures such as habitat loss and overexploitation. This phenomenon is increasing in Canada. The Province of Alberta has an expanding economy based significantly on the development of natural resources such as agriculture, oil and gas, forestry and nature-based tourism. Individual grizzly bears, having large home ranges, increasingly come into contact with all of these activities. Herrero (1994) showed that grizzly bear populations in Canadian national parks by themselves were probably all too small to have a high probability of long-term persistence, and therefore integrated management with surrounding provincial or territorial lands would be required. Within Banff, Yoho and Kootenay National Parks, Gibeau (1998) found that habitat effectiveness was significantly compromised by development. Whether land is managed as parks, commercial forests or privately, management practices must respond to the grizzlies' needs if these bears are to survive. There is an urgent need for scientific data to help land managers better understand the effects of human activities on grizzly bears.

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The response of grizzly bears to humans has been the focus of much research within the last 15 years. Most of these studies, however, have focused on one type of human activity such as roads (McLellan and Shackleton, 1988; Mace et al., 1996), forestry or other industrial activity (Archibald et al., 1987; McLellan, 1990), recreation (Jope, 1985; Gunther, 1990; Olson et al., 1990; Mace and Waller, 1996), or facilities (Mattson et al., 1987; Reinhart and Mattson, 1990). Few studies have reported the effects of multiple human activities (Mattson et al., 1987; McLellan and Shackleton, 1989a; Kasworm and Manley, 1990) and then, only using univariate analysis.

We document the way grizzly bears distribute themselves in relation to different human activities and development features based on sex, age class and habitat quality in a landscape where human presence is widespread. In this setting, grizzly bears may not be able to avoid humans and still find requisite resources. Using radio telemetry information, we tested the hypothesis that different sex and age classes of grizzly bears do not differ in their response to roads, trails, and major development features.

2. Study area

The study area encompassed the Bow River Watershed from its headwaters to approximately where it meets the prairies. This is 11,400 km^2 of mountainous terrain 50–180 km west of Calgary (a city of 800,000 people) in southwestern Alberta. The area includes a portion of Banff National Park (BNP) and adjacent Alberta Provincial lands known as Kananaskis Country. While neither jurisdiction allows grizzly bear hunting, bears are legally harvested from some adjacent lands. Differing agency mandates oversee preservation, industrial tourism, recreation, forestry, oil and gas extraction, mining and stock grazing. Towns and municipalities, native councils, commercial developers and residential owners diversify land administration even further.

Human presence is widespread both within and outside of BNP. Three towns, Banff, Lake Louise and Canmore are world-renowned tourist destinations that attract approximately 5 million visitors annually. In addition to the towns that support the tourism industry developments include a multitude of hotels, campgrounds and picnic areas, five golf courses, five downhill ski facilities and an extensive network of hiking, biking and equestrian trails.

The Trans Canada Highway (TCH), a high-speed, high-volume (21,000 vehicles per day, average daily summer traffic volume; Parks Canada, unpublished data) transcontinental transportation route, bisects the study area. The TCH is a 4-lane divided highway through much of the study area and 45 km through BNP has been fenced to keep wildlife off the road. Wildlife crossing structures have been placed throughout the fenced section to facilitate movement across the highway (Clevenger and Waltho, 2000). Several high-speed, two-lane paved roads serve as arterial transportation routes. Numerous two-lane paved secondary roads complete the transportation system through most of the low elevation valleys. Traffic volumes on these arterial and secondary paved roads are high during the day (>300 vehicles per h) but low at night (<50 vehicles per h) which is significantly different than the continuous high volume on the TCH (Gibeau and Herrero, 1998). There are few gravel roads in the study area. We know of no other area within occupied grizzly bear habitat in North America that has such an extensive network of high-speed, high-volume highways. The combination of a well-developed transportation system and elaborate infrastructure make the Bow River Watershed one of the most intensively developed landscapes in the world where a grizzly bear population still survives (Gibeau, 2000).

Topographic features include rugged mountain slopes, steep-sided ravines, and flat valley bottoms. The climate is continental with long, cold winters and short, cool summers. The aspect and elevation of the mountainous topography modifies climate somewhat. Topography, soil, and local climate strongly influence plant communities.

3. Methods

Between 1994 and 1998 we captured and radio-marked grizzly bears in the study area and monitored their movements. Individuals were equipped with either a conventional radio collar (Lotek Engineering, Newmarket, Ontario) or an ear tag transmitter (Advanced Telemetry Systems, Isanti, Minnesota). All radio collars were fitted with a breakaway cotton spacer (Hellgren et al., 1988) to ensure that collars would not be worn permanently. Through testing with radio collars placed in known locations we recorded an average telemetry error of 150 m.

We searched for collared bears at least once per week from the air, weather permitting, using a Bell Jet Ranger III helicopter or a STOL equipped Cessna 337 Skymaster. Aerial tracking followed the techniques of Mech (1983). Aerial fixes were established from an aircraft mounted GPS unit and later transformed to UTM coordinates (North American Datum, 1927) using the Geocalc Program (Blue Marble Graphics, 1993). We also located bears from the ground on a daily basis where possible using a portable receiver, roof mounted omni-directional antenna and three-element hand-held yagi antenna. Rugged mountain topography limited our ground-based search for collared bears to areas adjacent to roads and trails.

We used both air and ground radio telemetry data sets consisting of one relocation per day to avoid biases of over sampling and maximize independence between telemetry locations (Swihart and Slade, 1997; Alldredge et al., 1998). Our ground-based telemetry data was biased however, towards those areas where workers can travel. In this analysis we used ground-based telemetry data in some instances because the analysis was specific to areas where workers could travel, and sample sizes were larger than the aerial data set. Relocations were categorized by: (1) sex; (2) age: adult (> 5 years old) and subadult; (3) season: preberry (den emergence through 15 July) and berry (16 July through den entrance); (4) differences in hours of peak human activity both on the highways and trail system (Parks Canada unpublished data) being human active (08:00–17:00) versus human inactive (17:00–0:800) periods; (5) distance to high quality habitat: within (< 150 m, which is consistent with telemetry error), adjacent (150–300 m) or distant (> 300 m).

In the absence of a habitat suitability map for the study area we derived surrogate habitat values using Landsat Thematic Mapper satellite images transformed into a greenness band using the tasseled cap transformation (Crist and Cicone, 1984; Manley et al., 1992). Mace et al. (1999) found a strong selection by grizzly bears for areas of high greenness. We categorized the image into 12 classes of increasing greenness as an indicator of grizzly bear habitat. Use and expected values for each greenness class calculated from our aerial telemetry data set indicated that the four highest classes were used more than expected based on availability ($P=0.0002$; Gibeau, 2000). These four classes were combined into a single GIS map layer to represent preferred or high habitat quality.

The percentage of available vegetative cover was calculated for each 30-m pixel within the study area based on classified Landsat Thematic Mapper satellite images using a moving-window routine. We chose a 1.5-km-radius as a moving-window size which approximates the average daily feeding radius of an adult female grizzly bear in our study area (Gibeau, 2000). The resulting GIS map provided a measure of the percent hiding cover in the vicinity of each telemetry location.

We quantified human presence using the most recent data of human activity across the region (Gibeau, 1998). These GIS maps categorized vector, point and polygon data of all motorized and non-motorized human developments and facilities into high (> 100) and low (< 100) users per month (Gibeau, 1998) based on visitation records and expert opinion. These data became the basis for measuring the distance of telemetry locations to various human developments and features. We categorized human use as: (1) Trans Canada Highway, (2) high use paved roads, (3) high use trails, and (4) high use features (campgrounds, lodges, picnic area, etc.). Although there were several low use trails within the study area, most were located in association with either the TCH or a high use paved road. Any attempt to partition out the effects of low use trails were masked by these other roadways. There were too few gravel roads, low use roads, and low use features for meaningful analysis.

3.1. Analysis

The nearest distance (> 1 m) to each of the above four human use categories was calculated in a raster format with a 50-m pixel size using Idrisi® (Clark University, Worcester, MA) GIS software for each telemetry location. The resulting spreadsheet provided distances to four types of human uses, and percent hiding cover for every telemetry location categorized by sex, age, season, time of day, and habitat quality. For comparison, we generated a stratified sample of 2765 random points and calculated the nearest distance to each of the four human use categories for these locations as well.

Analysis of the distance data was complicated by the rugged mountainous topography. Distance measurements did not take into account intervening mountain ranges, therefore we had to impose distance limits to avoid measurements that were in fact in adjacent mountain valleys. We found the average distance between ridge tops for the major valleys in the Bow River Watershed to be 6.5 km. Therefore, we used half that distance (3.25 km) as a maximum to give a high probability that measurements were within the same mountain valley.

We used a Mann–Whitney U statistic to test whether the aerial and ground telemetry data sets, and the sample of random points, came from the same population. An unbalanced analysis of variance (ANOVA) was used to test both main effects and interactions among sex, age, season, distance to high habitat quality, and time of day for the measured distances to each of the four types of human uses. Profile plots were used to visualize the relationship between variables using estimated marginal means. Significance was accepted at $P<0.05$. The assumption of equal variance was met for the aerial telemetry data set only.

4. Results

We collected 4359 daily telemetry locations from 49 grizzly bears (15 adult male, seven subadult male, 19 adult female, eight subadult female) during the study. Slightly more than half of the locations were obtained from the ground ($n=2471$, 57%) compared to aerial locations ($n=1888$). There were statistically significant differences between the aerial and ground telemetry data sets ($P = 0.002$) in observed distances to high use paved roads, high use trails and high use features; however, not for the TCH ($P = 0.101$). Although the ground-based telemetry data was statistically different from the aerial data set, we report and interpret ground-based results because the analysis is specific to areas where workers could travel and ground-based telemetry may provide further biologically meaningful insights (Cherry, 1998; Johnson, 1999). Significant differences also existed between the aerial data set and the random sample in observed distances to the TCH ($P = 0.011$), high use paved roads ($P = 0.004$), high use trails ($P < 0.001$) and high use features ($P = 0.025$). Reported results are from the aerial telemetry data set, except where we specifically denote the ground-based data was used.

Differences between the percent hiding cover around telemetry locations (56%) and the random sample (22%) were evident ($P < 0.001$). While not statistically significant, males were found closer (67% of the time) to hiding cover than females (52%). Again, while no statistical significance was detected, adult males were found closer to cover (68%) than subadult males (56%). Adult (52%) and subadult (58%) females had similar use of hiding cover.

The distribution of distance measurements for most of the four types of human uses was found to be non-normal. However, the similar shapes of the distributions (symmetric to slightly right-skewed) resulted in the variables having similar variances (verified by the Levene's tests of the homogeneity of variance). Results of statistical tests were the same with both the original values and transformed values to normalize the data. Because ANOVA is robust to departures from normality and for clarity of presentation, we present results of original values. The corrected model for each of the four types of human uses was significant ($P < 0.025$). Due to model complexity, three- and four-way interactions were not considered. We report median distances to human developments and activities as they provide a better measure of central tendency than means when data are skewed (Table 1).

4.1. TCH

The average distance female grizzly bears were found from the TCH was greater than that for males or the random sample ($F_{7,121} = 17.21$; $P < 0.001$; Table 1). Differences between the sexes were also seen when we analyzed the proximity of high quality habitat ($F_{24,90} = 5.24$; $P = 0.024$). Females were located further than random from the TCH regardless of habitat quality. Males, on the other hand, were found closer than expected by chance to the TCH when within or adjacent to high quality habitat but further than random when distant from high quality habitat (Table 1). The population as a whole displayed little variation in its response to the TCH whether within, adjacent to, or distant from high quality habitat (Fig. 1a).

Clear differences were found between sex and age class in the ground-based data set ($F_{7,739} = 60.30$; $P < 0.001$). While both subadult and adult females and adult males were found further away from the TCH than random, subadult males were much closer to the TCH. The aerial data set characterized an almost identical pattern (Table 1) although no statistical significance was detected ($F_{7,121} = 2.58$, $P = 0.111$; power = 0.357).

The ground data set also depicted differences between the sexes and time periods ($F_{15,731} = 73.02$; $P < 0.001$). Females remained further from the TCH than random during both the human active and human inactive periods (Table 2). Although males were further away than random during the human active period, they were closer than random during the human inactive period. We did not have a sample of night time locations to test the aerial data set.

Table 1
Median distance (m) to human developments measured from aerial telemetry locations of grizzly bears in the Bow River Watershed, Alberta, 1994–1998

	Stratified random sample	Both sexes	Males						Females					
						High quality habitat						High quality habitat		
			All males	Adult	Subadult	Within	Adjacent	Distant	All females	Adult	Subadult	Within	Adjacent	Distant
TCH[a]	1432	1966	1741	1810	649[b]	905[b]	1134	1999	2148	2331	2071[b]	2294	2040[b]	2199[b]
Paved roads	1193	850	781	771	828	618	320[b]	951	900	951	800	868	943	1050[b]
High use trails	1031	750	747	701	889	781	570	989	750	743	849	743	919	1145
Features	1791	1748	1602	1603	1521	1471	2022	2438	1808	1834	1550	1697	1692	1978

[a] Trans Canada Highway.
[b] Small sample size (< 30 locations).

4.2. High use paved roads

No statistical difference was detected between female and male distances to high use paved roads ($F_{7,496} = 0.20$; $P = 0.657$; power = 0.073) although both sexes were both closer than random (Table 1). Conclusions from the aerial data set may not be reliable because of the high probability of committing a Type II error, given that the statistical power indicated little chance of detecting a difference due to the small sample. Similar to the TCH findings, the same pattern of differences between the sexes depending upon the proximity of high quality habitat, was again evident with high use paved roads. Females remained much further from high use paved roads whether within, adjacent to, or distant from high quality habitat. Males on the other hand, were found much closer than random to high use paved roads when within or adjacent to high quality habitat, but further away from high use paved roads when distant from high quality habitat (Table 1). This relationship was statistically significant only in the ground data set ($F_{47,1736} = 18.88$; $P < 0.001$).

Differences were also seen between the sexes and time periods ($F_{15,1829} = 14.65$; $P < 0.001$). Females were further from high use paved roads during the human active and human inactive periods than males. Males were further from high use paved roads during the human active period, but closer during the human inactive period (Table 2).

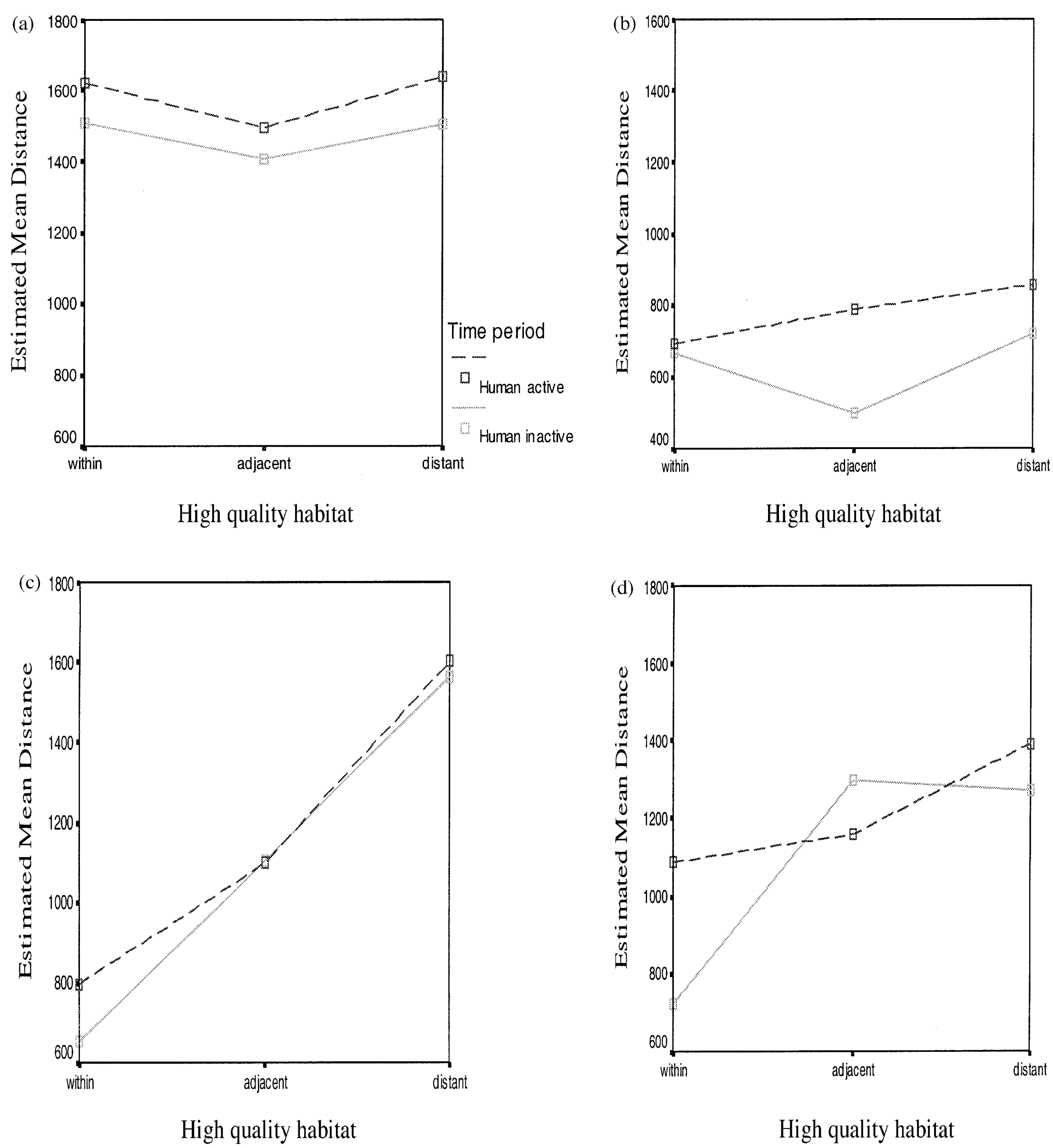

Fig. 1. Profile plots of the interaction between high quality habitat and time period for (a) TCH, (b) high use paved roads, (c) high use trails, and (d) high use features, for grizzly bears in the Bow River Watershed, Alberta, 1994–1998.

Table 2
Median distance (m) to human developments by time period, measured from ground-based telemetry locations of grizzly bears in the Bow River Watershed, Alberta, 1994–1998

	Stratified random sample	Males time period		Females time period	
		Human active	Human inactive	Human active	Human inactive
TCH[a]	1432	1626	1166	2185	2007
Paved roads	1193	583	391	604	566
High use trails	1031	901	860	500	550
Features	1791	1259	1204	894	604

[a] Trans Canada Highway.

4.3. High use trails

No statistical difference was detected between female and male distances to high use trails ($F_{7,1561}=0.07$; $P=0.784$; power $=0.059$) although both sexes were both closer than random (Table 1). Although not statistically significant ($F_{40,1264}=2.31$; $P=0.100$; power $=0.470$), bear use in association with high use trails also depended upon the proximity of high quality habitat. In both cases, conclusions from the aerial data set may not be reliable because of the high probability of committing a Type II error, given that the statistical power indicated little chance of detecting a difference due to the small sample. Female bears within or adjacent to high quality habitat were closer to high use trails than if distant from high quality habitat. Males were also closer to trails when within or adjacent to high quality habitat than when they were distant from high quality habitat (Table 1). The ground telemetry data set confirmed the same pattern and was highly significant ($F_{46,1999}=33.55$; $P<0.001$).

A significant difference was detected in distance to high use trails between the sexes and time periods ($F_{15,2254}=13.18$; $P<0.001$). Females were closer than males to high use trails during both the human active and human inactive periods (Table 2). Overall, there was a trend for bears to be further away from developments during human active periods and closer during the human inactive period when the proximity of high quality habitat is accounted for (Fig. 1c).

4.4. High use features

While not significantly different ($F_{7,794}=0.05$; $P=0.815$; power $=0.056$), female distance to high use features was further than that of males or random (Table 1). Both females and males were found closer to features than random when within high quality habitat, but further than random when distant from high quality habitat (Table 1). Again, conclusions from the aerial data set may not be reliable because of the high probability of committing a Type II error, given that the statistical power indicated little chance of detecting a difference due to the small sample. The same pattern is seen in the ground-based data set although the differences between the sexes are much more pronounced ($F_{47,1756}=9.21$; $P<0.001$).

Although no statistical significance was detected in the aerial data set between the age classes and distance to features ($F_{7,794}=1.42$; $P=0.234$; power $=0.221$), a highly significant pattern is evident in the ground data set ($F_{7,1958}=33.32$; $P<0.001$). Adults were found further away than expected from features, while subadults were closer to features (Table 1).

The ground data set also depicted significant differences in distance to features between the sexes by time periods ($F_{7,1958}=44.50$; $P<0.001$). Females were closer to features than males during both the human active and human inactive period. Males remained some distance from features during both the human active and human inactive periods (Table 2). Generally, bears were found closer to high use features when within high quality habitat and when humans were inactive (Fig. 1d).

With all four types of human developments we found differences between the two seasons; however, we found statistical significance only in distance from features ($F_{7,794}=4.80$; $P=0.029$). While no consistent pattern emerged, a weak trend of the data depicted subadults closer to human development in preberry season than berry season, while the opposite was true for adults. It seems likely that any observed variation in seasonal distance to human developments would be related to seasonal changes in food value arising from the progression of plant phenology.

5. Discussion

Wildlife response to humans and our activities occur in different circumstances, and in differing magnitudes (Whittaker and Knight, 1998). Wildlife also behave differently in different locations and during different activities, and the learned outcomes of all these interactions affect subsequent interactions (Gilbert, 1989). Our data establish correlations, not causal relationships between various human stimuli and observed grizzly bear locations. We make inferences about causality and grizzly bear response based upon our data and relevant literature.

Of the four types of human developments we investigated, the TCH was avoided most by grizzly bears. Female bears avoided the busy freeway regardless of the habitat quality or time of day. Males, and especially subadult males, were found closer to the TCH when within or adjacent to high quality habitat and during the human inactive period. These observed responses may not be solely due to the TCH, but to the higher overall density of humans associated with the valley that includes the TCH. Greater use of hiding cover by males may be part of the strategy used to take advantage of high quality habitat near roads.

Several authors believe that grizzly bears become accustomed to predictable occurrences (Herrero, 1985; Jope, 1985), including traffic (McLellan and Shackleton, 1989b) although our results have suggested otherwise for high-speed, high-volume highways. There is a point when the combination of traffic volume and highway configuration overrides a bear's attraction to high quality habitats (Fig. 1a). Between 1994 and 1998 none of the radio collared adult female bears crossed the TCH and only 2 radio collared males regularly crossed (Gibeau, 2000). During 1999 and 2000 a new radio-collared adult female did cross in the fenced section of the TCH using the wildlife crossing structures. Additionally, two highly habituated young females also crossed an unfenced section of the TCH in the vicinity of the town of Lake Louise (Gibeau unpublished data). After 7 years of research we conclude that the TCH appears to be a barrier to adult female grizzly bear movement.

The same pattern of grizzly bear response to paved roads was seen as to the TCH, although both sexes were found closer than a random pattern would predict. Females remained further than males from paved roads regardless of the habitat quality or time of day. Males were found closer to paved roads when within or adjacent to high quality habitat and during the human inactive period.

Avoidance of roads by grizzly bears has been documented by Tracey (1977), Harding and Nagy (1980), Archibald et al. (1987), Mattson et al. (1987), McLellan and Shackleton (1988), Kasworm and Manley (1990), and Mace et al. (1996). We too documented bears further from roads when distant from high quality habitat which we interpret as avoidance behavior. In this environment, however, bears were found closer to paved roads than would be predicted, presumably to acquire high quality food resources. High quality habitat is a strong attractant. Mace et al. (1996) demonstrated that avoidance of roadside buffers by grizzly bears generally increased with traffic levels and road densities, but bears did use important habitats adjacent to roads with low to moderate traffic levels. This neutral use, or positive selection toward habitats near roads implied that important habitat resources possibly occurred near roads in their study area also.

Unlike paved roads that were located in valley bottoms and good quality habitats, high use trails were widely distributed throughout all types of habitats within the study area. Bears were found closer to trails during the human inactive period when within high quality habitat and further from trails when distant from high quality habitat (Fig. 1c). In the Swan Mountains Montana, Mace and Waller (1996) concluded that grizzly bears using hiking trails have become negatively conditioned to human activity and that they minimized their interaction with recreationalists by spatially and temporally avoiding high use areas. Our data suggest the same pattern in the absence of high quality habitat.

Kasworm and Manley (1990) reported that, overall, grizzlies were displaced less by trails than by roads. Our results suggest otherwise for this study area. Our observed avoidance of high use trails when distant from high quality habitat may be a reflection of a greater opportunity for bears to select high quality habitat in the relative absence of humans. In our study area, grizzly bears may not have the opportunity to truly "avoid" paved roads without forfeiting access to much of the high quality habitats.

The distribution of grizzly bears in relation to development features was less uniform. While distance measurements were not as great as for the TCH, bear response to high use features were still double those of paved roads or high use trails. Females, and especially subadult females, were found closer to features when within or adjacent to high quality habitat during the human inactive period. Males, on the other hand, remained further away from features regardless of habitat quality or time of day (Table 2).

Bears were more willing to take advantage of high quality habitat near features while humans were inactive. While this trend was evident for all types of human developments, it was most pronounced in association with features (Fig. 1d). Mattson et al. (1987) and Reinhart and Mattson (1990) found that habitats were substantially under used especially during the day near town-sites and recreational developments. Our results show that grizzly bears were more likely to use roads, trails and human facilities at night or when unoccupied. This is consistent with other studies (Harting, 1985; Nadeau, 1987; McLellan and Shackleton, 1988; Gunther, 1990).

Our data indicate an inverse relationship between the sexes in response to vehicles and traffic noise (TCH and paved roads) compared to the response to human settlement and encountering people (high use trails and features). Female bears were found further away than males in relation to vehicles and traffic noise, yet found closer than males to human settlement and places where people may be encountered. Females were also less willing to take advantage of the high quality habitats that were in roaded valley bottoms. We were unable to determine whether this was a result of dominance hierarchy, but displacement into sub-optimal habitats and/or reduced feeding efficiency may affect net energy intake and reproductive output.

One important yet confounding variable, both in the literature and within our data, was the level of habituation (Whittaker and Knight, 1998) of some individuals. Habituation (Herrero, 1985) may permit some bears to exploit habitats near roads, trails and developments, especially if human use is spatially and temporally predictable (Tracey, 1977; Jope, 1985; McLellan and Shackleton, 1989a; Olson et al., 1990). Several studies have suggested there are differences among sex, age and reproductive classes in the likelihood and level of habituation to humans (Olson et al., 1990; Mattson, 1990). Our observations on responses of grizzly bears to various human developments reflect some of these differences, even though the majority of study bears were not considered habituated.

Social structure may also have a bearing on spatial distribution of a bear population. In Yellowstone National Park, Mattson et al. (1987) demonstrated that cohorts of subordinate bears were found in poorer-quality habitats near developments, displaced by more dominant classes, particularly adult males. McLellan and Shackleton (1988) also determined that adult males used remote areas whereas adult females and some subadults used areas closer to roads. While our results pointed to differential use by sex and age, we were unable to determine whether this distribution is a natural phenomenon or the result of competition for space with humans.

We conclude from our observations and the literature, that there were significant differences in grizzly bear response to roads, trails and major development features categorized by sex, age class, proximity of high quality habitat and time of day. High human presence is likely to be the reason most grizzly bears are unwilling to use habitats near busy transportation corridors. This avoidance behavior was strongest in the adult segment of the population where we believe males selected for high quality habitats and an absence of humans. Those males that were willing to exploit high quality habitat near roads, did so at night and where hiding cover was present. Adult females were the most risk averse cohort, choosing to avoid humans instead of seeking out the highest quality habitats. Adult females selected areas with a high degree of security for raising cubs (Gibeau et al., 2001), which in some cases also meant avoiding adult males. With the safest and highest quality habitats taken up by adult males and resident females, subordinate bears including some adult females, were forced to use sub-optimal habitats including those with high human presence. Our data demonstrated that subadults were almost always closer to humans than adults were. Unable to successfully compete elsewhere, these bears were relegated to using habitats close to people and developments. Bears in close proximity to humans are more apt to become habituated to people. While habituated bears appear to successfully use habitats near humans, they also are most likely to die at the hands of humans (Mattson et al., 1992; McLellan et al., 1999).

6. Management implications

Research from Yellowstone National Park demonstrated that avoidance of roads and developments by grizzly bears probably resulted in adult females in poorer condition and consequently, higher mortality rates and lower fecundity than other cohorts (Mattson et al., 1987). The reproductive potential of any population resides in the adult female cohort. In a landscape as intensely developed as the Bow River Watershed, adult female grizzly bears are influenced most by human activities and development. Providing adult female grizzly bears with the highest level of protection possible should be a management priority.

Mace et al. (1996) also found that spatial avoidance of roads increased and survival decreased as traffic levels, road densities and human settlement increased. Based on our findings and those from other grizzly bear ecosystems, it will be difficult to maintain a contiguous grizzly bear population in the Central Canadian Rocky Mountains. In an era when humans are having a significant influence upon the landscape even within areas considered to be refugia, agency managers need to delineate important sites for bears and protect them from disturbance. The key to this is managing human use.

Habitat fragmentation and physical barriers pose what many conservation ecologists consider the greatest risk to maintaining species diversity (Ralls et al., 1986; Forman and Alexander, 1998). Both high traffic volumes and habitat alienation make the TCH and the Bow River Valley an extremely hostile environment for grizzly bears. This is most acute for adult females where they not only have compromised access to high quality habitat but also face an almost impenetrable barrier to movement. Already, a significant amount of time, energy, and money has gone into the design, placement and construction of crossing structures for wildlife passage across the TCH (Leeson, 1996; Clevenger and Waltho, 2000). Given our results, the question remains however, as to how grizzly bears will get to the mouth of these structures in order that they may cross the highway. Further, is it possible to mitigate highway effects for grizzly bears if they are repelled by highways and fail to even get close to them? Currently, the combination of intense sensory disturbance from high traffic volumes and the overall high density of humans precludes most grizzly bears from being in the vicinity of the TCH. For bears to have the possibility of using these crossing structures the density of humans must be reduced. Given grizzly bear's large home ranges, significant potential currently exists for permanent habitat and population fragmentation to occur. Management agencies must maintain access to high quality habitat, especially for adult females. An adaptive management approach will be crucial as we continue to gain knowledge of grizzly bear response to highways.

The future of any population is found in the subadult cohort. As in other ecosystems, subadult grizzly bears in the Bow River Watershed are predisposed to interact with humans. This increased exposure to humans translates into a greater danger of being killed by humans. Every effort must be made to maintain and encourage wary behavior in vulnerable individuals and cohorts.

Many of the management techniques needed to maintain population viability are known from experiences in the United States and Canada, and need only to be applied and refined in this study area (Herrero et al., 1986; Gunther, 1995; Schirokauer and Boyd, 1998). These include seasonal restrictions on human use of high quality habitat, locating trails and facilities away from such habitat and managing habituation. The need to control human access and to restrict development has been acknowledged in Banff National Park and to a lesser extent in Kananaskis Country, although the mechanisms for doing so are under development. Strict control of human access can be achieved by applying seasonal area closures, seasonal trail closures, day use only restrictions, travel limited to mid day only and restrictions on party size. In the end, the most difficult aspect of making real gains in grizzly bear conservation may be mustering the social and political will to implement change.

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References

Allredge, J.R., Thomas, D.L., McDonald, L.L., 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3, 237–253.

Archibald, W.R., Ellis, R., Hamilton, A.N., 1987. Responses of grizzly bears to logging truck traffic in the Kimsquit River Valley, British Columbia. International Conference on Bear Research and Management 7, 251–257.

Clevenger, A.P., Waltho, N., 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14, 47–56.

Cherry, S., 1998. Statistical tests in publications of The Wildlife Society. Wildlife Society Bulletin 26, 947–953.

Crist, E.P., Cicone, R.C., 1984. Application of the tasseled cap concept to simulated thematic mapper data. Photogrammetric Engineering and Remote Sensing 50, 343–352.

Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29, 207–231.

Gibeau, M.L., 1998. Grizzly bear habitat effectiveness model for Banff, Yoho, and Kootenay National Parks, Canada. Ursus 10, 235–241.

Gibeau, M.L., 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. PhD dissertation, Resources and the Environment Program, University of Calgary, Calgary AB. Canada.

Gibeau, M.L., Herrero, S., 1998. Roads, rails, and grizzly bears in the Bow River Valley, Alberta. In: Evink, G.L., (Ed.), Proceedings of the International Conference on Ecology and Transportation. Florida Department of Transportation, Talahassee, Florida, USA, pp. 104–108.

Gibeau, M.L., Herrero, S., McLellan, B.N., Woods, J.G., 2001. Managing for grizzly bear security areas in Banff National Park and the Central Canadian Rocky Mountains. Ursus 12 (in press).

Gilbert, B.K., 1989. Behavioral plasticity and bear-human conflicts. In: Bear-People Conflicts. Proceedings of a Symposium on Management Strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Canada, pp. 1–8.

Gunther, K.A., 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. International Conference on Bear Research and Management 8, 73–78.

Gunther, K.A., 1995. Bear management in Yellowstone National Park, 1960–93. International Conference on Bear Research and Management 9, 549–560.

Harding, L., Nagy, J.A., 1980. Responses of grizzly bears to hydrocarbon exploration on Richards Island, Northwest Territories, Canada. International Conference on Bear Research and Management 4, 277–280.

Harting, A.L., 1985. Relationships between activity patterns and foraging strategies of Yellowstone grizzly bears. MS thesis, Montana State University, Bozeman, Montana.

Hellgren, E.C., Carney, D.W., Garner, N.P., Vaughan, M.R., 1988. Use of breakaway cotton spacers on radio collars. Wildlife Society Bulletin 16, 216–218.

Herrero, S., 1985. Bear Attacks: Their Causes and Avoidance. Winchester Press, Piscataway, New Jersey.

Herrero, S., 1994. The Canadian National Parks and grizzly bear ecosystems: the need for interagency management. International Conference on Bear Research and Management 9, 7–21.

Herrero, S., McCrory, W., Pelchat, B., 1986. Using grizzly bear habitat evaluation to locate trails and campsites in Kananaskis Provincial Park. International Conference on Bear Research and Management 7, 179–186.

Johnson, D.H., 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63, 763–772.

Jope, K.L., 1985. Implications of grizzly bear habituation to hikers. Wildlife Society Bulletin 13, 32–37.

Kasworm, W.F., Manley, T.L., 1990. Road and trail influences on grizzly bears and black bears in northwest Montana. International Conference on Bear Research and Management 8, 79–84.

Leeson, B.F., 1996. Highway conflicts and resolutions in Banff National Park, Alberta, Canada. In: Evink, G.L., Garrett, P., Zeigler, D., Berry, J. (Eds.), Trends in Addressing Transportation Related Wildlife Mortality. Proceedings of the Transportation Related Wildlife Mortality Seminar, State of Florida DOT, Environmental Management Office, Tallahassee, Florida, USA.

Mace, R.D., Waller, J.S., 1996. Grizzly bear distribution and human conflicts in Jewel Basin hiking area, Swan Mountains, Montana. Wildlife Society Bulletin 24, 461–467.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., Zuuring, H., 1996. Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana. Journal of Applied Ecology 33, 1395–1404.

Mace, R.D., Waller, J.S., Manley, T.L., Ake, K., Wittinger, W.T., 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology 13, 367–377.

Manley, T.L., Ake, K., Mace, R.D., 1992. Mapping grizzly bear habitat using Landsat TM satellite imagery. In: Remote Sensing and Natural Resource Management. Proceedings of the Fourth Remote Sensing Applications Conference. US Forest Service, Orlando, Florida, USA, pp. 231–240.

Mattson, D.J., 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8, 33–56.

Mattson, D.J., Knight, R.R., Blanchard, B.M., 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. International Conference on Bear Research and Management 7, 259–273.

Mattson, D.J., Blanchard, B.M., Knight, R.R., 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56, 432–442.

McLellan, B., 1990. Relationships between human industrial activity and grizzly bears. International Conference on Bear Research and Management 8, 57–64.

McLellan, B.N., Shackleton, D.M., 1988. Grizzly bears and resource extraction industries: effects of roads on behavior, habitat use, and demography. Journal of Applied Ecology 25, 451–460.

McLellan, B.N., Shackleton, D.M., 1989a. Immediate reactions of grizzly bears to human activities. Wildlife Society Bulletin 17, 269–274.

McLellan, B.N., Shackleton, D.M., 1989b. Grizzly bears and resource-extraction harvesting and road maintenance. Journal of Applied Ecology 26, 371–380.

McLellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkinen, W.L., Kasworm, W.F., 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63, 911–920.

Mech, L.D., 1983. Handbook of Animal Radio-tracking. University of Minnesota Press, Minneapolis, Minnesota, USA.

Nadeau, M.S., 1987. Habitats, trail, and campground situations associated with human-grizzly confrontations in Glacier National Park, Montana. MS thesis, University of Montana, Missoula, Montana.

Olson, T.L., Gilbert, B.K., Fitkin, S.H., 1990. Brown Bear and Human Activity at Salmon Streams in Katmai National Park, Alaska (Final Report. Interagency Agreement IA9700-7-8028). Utah State University, Logan (123 pp.).

Ralls, K., Harvey, P.H., Lyles, A.M., 1986. Inbreeding in natural populations of birds and mammals. In: Soule, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts, USA, pp. 35–56.

Reinhart, D.P., Mattson, D.J., 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. International Conference on Bear Research and Management 8, 343–350.

Schirokauer, D.W., Boyd, H.M., 1998. Bear-human conflict management in Denali National Park and Preserve, 1982–94. Ursus 10, 395–403.

Swihart, R.K., Slade, N.A., 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2, 48–63.

Tracey, D.M., 1977. Reaction of wildlife to human activity along Mount McKinley National Park road. MS thesis, University of Alaska, Fairbanks, Alaska.

Whittaker, D., Knight, R.L., 1998. Understanding wildlife response to humans. Wildlife Society Bulletin 26, 312–317.