

Grizzly bear associations along the eastern slopes of Alberta

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Abstract: We used Doncaster's test to differentiate home range overlap in range use from mutual attraction in grizzly bears (*Ursus arctos*) based on global positioning system (GPS) telemetry data. From a sample of 61 collared bears, 404 pairs of GPS locations placed 2 or more bears ≤ 500 m from each other at about the same time (within 3 hr). From these 404 pairs, 68 were significantly positive associations (mutual attraction) in which 65% were male–female (MF) and 35% were the same sex. Most MF associations involved adults. Male and female bears had associations with 1.8 and 1.2 partners/year, respectively. Associations between males occurred twice as often in the pre-berry season than in the berry season, whereas female–female (FF) associations occurred more frequently in the berry season. The length of same-sex associations was significantly shorter than MF associations. Fifty-one percent of MF pairs associated more than once within a single year. For MF associations, the mean distance between individuals was 152 m. Our findings suggest that grizzly bears can spend a considerable amount of time interacting with conspecifics and that behavioral interactions between grizzly bears are more complicated than we understand. Human activity that affects grizzly bear associations could disrupt social behavior and ultimately reproduction.

Key words: Alberta, Doncaster's test, grizzly bear, home range overlap, interactions, intraspecific, mating, mutual attraction, *Ursus arctos*

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By studying intraspecific associations, biologists can better understand and predict how human activity might affect the social structure of a species. If social behavior is disrupted, the social structure of a population and ultimately reproduction may be affected. There are many reasons why conspecifics associate. Interactions may occur due to home range overlap (Doncaster 1990), as happens around travel corridors or high quality habitats. Of most interest are interactions that involve mutual attraction in which animals interact for mating, or for other biological reasons (family groups), in which the closeness of locations cannot be explained by overlap of frequently utilized areas.

Few studies have been able to unobtrusively examine in detail the social behavior of grizzly bears (*Ursus arctos*) in forested ecosystems. To be effective, spatial

and temporal information from many individuals need to be collected simultaneously (Mace and Waller 1997). This is often difficult for grizzly bears because they are usually found in relatively low densities in remote, rugged, forested areas.

Social behavior in which grizzly bears occurred in dense numbers in open habitat have been documented (Hornocker 1962, Craighead et al. 1969), and these studies revealed that sometimes a large percent of time was spent interacting with conspecifics. Other work that addressed grizzly bear associations includes observations of captive grizzly bears (Koene et al. 2002), incidental mating observations (Mundy and Flook 1964, Herrero and Hamer 1977, Clevenger et al. 1992), and inferred interactions based on VHF (very high frequency) telemetry locations (Wielgus and Bunnell 1994, 1995; Mace and Waller 1997). When association is inferred from the closeness of telemetry points, this approach assumes that bears close together interact in some way and are not in the same area due to chance overlap of utilized areas. To our knowledge, no researchers have

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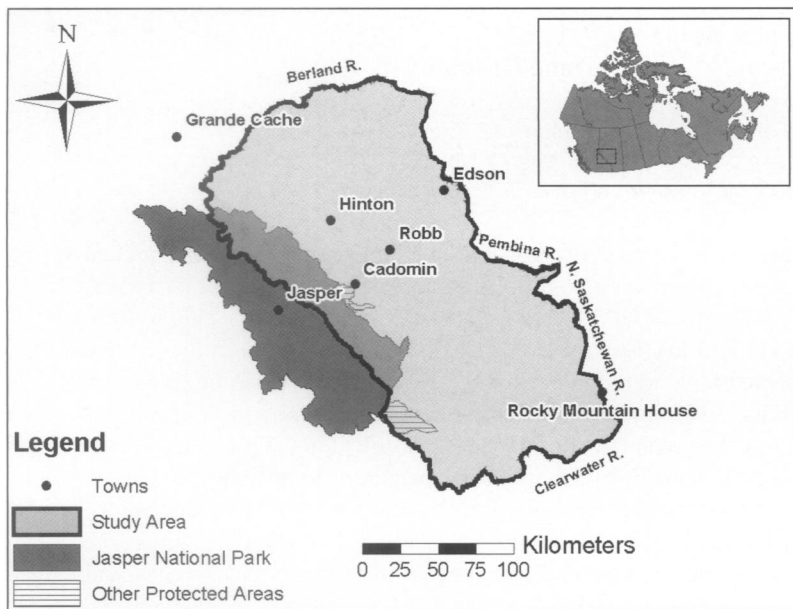


Fig. 1. Study area for investigating grizzly bear associations using data from GPS (global positioning system) collars in west-central Alberta, Canada, 1999–2003.

differentiated associations resulting from home range overlap from those resulting from mutual attraction of grizzly bears, based on GPS data.

We investigated intraspecific associations among GPS-collared grizzly bears along the eastern slopes of the Rocky Mountains in Alberta, Canada. We reviewed these data on both the population and individual bear-pair scale. The key objective of the population analysis was to use a method proposed by Doncaster (1990) to statistically distinguish bears close together by chance (home range overlap associations) from those actively associating (mutual attraction associations). We further examined the mutual attraction associations on an individual bear-pair basis. Sex, age, season, genetic relationship, frequency, and duration of associations were examined.

Study area

Our study area was located along the eastern slopes of the Rocky Mountains in west-central Alberta (Fig. 1). Other grizzly bear studies were conducted in this area in the 1970s (Pearson and Nolan 1976, Russell et al. 1979), north of this area (Nagy et al. 1989), and most recently south of our study area (Gibeau 2000; S. Herrero, M.L. Gibeau, S. Stevens, and B. Benn, 2003, Eastern slopes grizzly bear project (ESGBP): Brief update, University of Calgary, Calgary, Alberta, Canada). Our 37,144 km² study area was bordered by the Clearwater River in the

south, the Berland River in the north, and by the Queen Elizabeth mountain range in Jasper National Park to the west. Portions of the Pembina River, North Saskatchewan River, and secondary rivers and creeks defined the eastern boundary. Elevations within the study area ranged from 3,012 m in the western mountainous areas and declined eastwards from the foothills to an elevation of 984 m. This elevational gradient resulted in a diversity of habitat types and ecosystems that included glaciers, mountains, alpine and sub-alpine meadow, wet meadow complexes, and forests dominated by coniferous species to mixed wood forests.

Protected areas comprised approximately 19% of this study area (Jasper National Park, Whitegoat Wilderness Area, and Whitehorse Wildlands Provincial Park). Outside these protected areas the full range of human activities

and disturbances were found, including forest harvesting, oil and gas exploration and development, mining, hunting, trapping, and all-terrain vehicle use. An extensive road network from resource extraction activities as well as seismic lines associated with energy exploration was present.

Methods

Between 1999 and 2003, we captured and collared 61 unique grizzly bears including both adults (≥ 5 yrs old) and subadults (< 5 yrs old) using helicopter aerial darting or foot snares (Cattet et al. 2003a,b). Each bear was fitted with either a Televilt (Lindesberg, Sweden) Simplex GPS radiocollar or an Advanced Telemetry Systems (Isanti, Minnesota, USA) GPS radiocollar. All capture efforts followed procedures accepted by the Canadian Council on Animal Care for the safe handling of bears. Research protocols were also reviewed and approved by the Animal Care Committee at the Western College of Veterinary Medicine in Saskatoon, Saskatchewan. We programmed the majority of radiocollars ($n = 37$) to acquire locations at 4-hr time intervals; however, some collars were programmed for 2-hr intervals ($n = 5$), 12-hr intervals ($n = 2$), or 2 or 3 different intervals ranging from 1–5 hrs ($n = 21$). Ninety-seven percent of all locations used in this analysis were 3-dimensional (x , y , and z) with degree of precision scores (DOP) < 8 . We divided the

year into 2 seasons, pre-berry (den emergence to 31 Jul) and berry (1 Aug to denning).

Genetic relationships were inferred from age and DNA microsatellite data. Ages were determined from an extracted premolar tooth, and allele frequencies from 15 loci obtained from hair (Paetkau and Strobeck 1994). A parent-offspring relationship was assumed if an associating bear pair was at least 5 years apart in age and matched at 1 allele for all 15 loci. We defined littermates as bears being the same age and matched at 1 allele at 11 loci (15 loci \times 75%).

Population analysis

We estimated whether nearness of bears in space (termed *spatial linkage*) and time (termed *temporal pairing*) could be explained by chance overlap of intensely used habitat areas such as kill sites or movement corridors. We used the test of Doncaster (1990) to estimate the probability that nearness of temporally paired points (a potential association) was due to chance overlap of mutually utilized habitat areas. If this probability was below a cutoff value (0.05), an association between bears was declared. For each paired sequence of points, if observations were within a critical distance of <500 m, they were classified as spatially linked. If locations were taken at the same time or close together (<3 hrs apart), they were defined as being paired temporally. We defined an association as the distance at which 2 bears would be aware of each other's presence and considered this to be 500 m. We tabulated frequencies of points as paired temporally-spatially linked ($f_{\text{paired-linked}}$), paired temporally-not spatially linked ($f_{\text{paired-not linked}}$), unpaired temporally-spatially linked ($f_{\text{unpaired-linked}}$), and unpaired temporally-not spatially linked ($f_{\text{unpaired-not linked}}$). If there were no association, temporally paired points (spatially and non-spatially linked) should have been independent of the temporally unpaired points (spatially and non-spatially linked). Independence was addressed using a 2×2 contingency table with time (paired or unpaired) as the columns and spatial (linked or unlinked) as the rows (Doncaster 1990). Under the assumption of independence, expected values were generated for each row and column of the contingency table. From this, hypothesis tests were formulated for positive association ($H_0: f_{\text{paired-linked}} \leq \hat{f}_{\text{paired-linked}}$, $H_a: f_{\text{paired-linked}} > \hat{f}_{\text{paired-linked}}$) and negative association ($H_0: f_{\text{paired-linked}} \geq \hat{f}_{\text{paired-linked}}$, $H_a: f_{\text{paired-linked}} < \hat{f}_{\text{paired-linked}}$). A Fisher exact test was used to estimate the 1-tailed probability of the null hypothesis. The Fisher exact test allows 1-tailed hypotheses tests and is robust to low cell

sample sizes that potentially bias chi-square statistics (Agresti 1990).

This comparison analysis was conducted for combinations of all bear pairs in which 95% kernel home range (Worton 1989) overlap was >0 using a batch program in SAS statistical package (SAS Institute 2000). Bear pairs were initially categorized as a positive or negative association depending on whether the observed number of locations was less than or greater than that expected by chance (from the contingency table analysis). In the case in which both the observed and expected values were 0 (bears did not come within the critical distance in paired or unpaired time), the association was rated as null and not considered further. Analyses were stratified by pre-berry or berry season to test for differences in seasonal association. Significance of statistical tests was evaluated at $\alpha = 0.05$.

Due to potential error in GPS locations, and because an incomplete path is generated when several hours occur between consecutive points, we could not be certain when bears came within the 500 m cutoff distance. In addition, the GPS collars were set to obtain locations at different times of the day, which meant that differences in paired reporting times between bears could be as long as 3 hrs. Because each of these constraints is subjective, we attempted a population level analysis to determine the sensitivity of the Fisher test to cutoff distance and differences in reporting times in detecting positive or negative association. For this, the test was repeated at a 2,000 m cutoff distance and median probabilities associated with positive and negative association (for bear pairs with significant associations as determined at 500 m) were assessed. In addition, the analysis was stratified by differences in reporting times of <1 hr and >1 hr. Sensitivity of the Fisher test probability to distance, such as an increase in probabilities of the null hypothesis with distance, would suggest that association was only observable at close distances and that subjective choice of cutoff distance would influence whether an association was detected. In contrast, less sensitivity would suggest a larger scale of association and lower test sensitivity to cutoff distance.

Individual bear-pair analysis

To examine associations on an individual bear-pair scale, we began with the significant bear pairs identified from the Doncaster test and further refined the selection criteria to obtain the best possible location data with reference to time.

Because collars were not all programmed to collect simultaneous locations, an assortment of acquisition

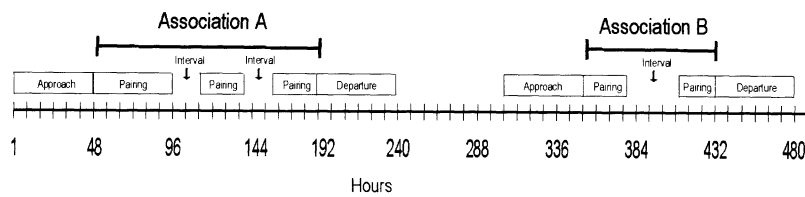


Fig. 2. Schematic of 2 multiple associations showing approach, intervals, pairings, and departure periods.

times occurred. We created a scheduled time separation (STS) variable that reflected the actual difference in acquisition times between individual collar pairs. Although the initial criteria to identify an association was set at <500 m and 3 hrs apart, within that 3-hr window, collar pairs could have STS values of 0.0, 0.5, 1.0, or 2.0 hrs. To obtain paired locations for a specific bear pair that yielded the closest possible locations in time, we restricted the data extraction by applying the specific STS value for each collar pair.

For example, for bears scheduled to acquire data at the same time (0 STS), we used only those locations that occurred <0.6 hrs of each other. The 0.6-hr buffer was used because 99% of locations were obtained by 0.6 hrs after the scheduled acquisition time. Similarly for other collar pairs, we used only those locations occurring <0.6 hrs of their STS. Collar pairs with STS values of 0 had almost simultaneous locations, while those with STS of 2 had locations obtained up to 2.6 hrs apart.

We defined an association as beginning at the location where 2 bears were <500 m apart and ending at the location prior to the first location where bears were >500 m apart, if this condition persisted for >48 hrs. Within an

association, pairings were defined as that time in which bears were continuously <500 m apart. There could be several pairings within an association, or an association might consist of a single pairing. We termed the time between pairings an interval (Fig. 2). Associations were classified as male–female (MF), female–female (FF), or male–male (MM).

To examine movements immediately preceding and following an association, we defined the 48 hrs before an association as the approach period and the 48 hrs after the association ended as the departure period (Fig. 2). Within an association, missing data was ignored unless it spanned more than 48 hrs, at which time the association was considered ended, corresponding with the defined end of the departure period.

In an attempt to identify any following behavior during the different phases of an association, we used the heading between a bear's successive locations to develop a relative indicator of paired movement. That indicator was calculated as $[\text{absolute value } ((-1 \times (\text{azimuth bear1} - \text{azimuth bear2})) - 180)] / 180$. Statistics were calculated with Systat Version 8.0 (SPSS Inc., Chicago, Illinois, USA) at a significance level of 0.05. Rates of movements and the directional index during the different phases of an association were examined with an ANOVA and a Kruskal-Wallis test, respectively. A Mann-Whitney test was used to indicate differences in association duration, and a *t*-test was used to identify differences in age and sex.

Results

Population analysis

We documented 404 pair-wise comparisons of bears in which home range overlap was > 0. Of these pair-wise comparisons, we detected 102 associations; 68 were significant positive associations (mutual attraction), 34 were non-significant positive associations (home range overlap), and 4 were negative association of which none were significant (when evaluated at 500 m and locations within 3 hrs of each other). Similar ratios of sex pairing were observed using paired locations from paired time separations of <1 hr and >1 hr (Table 1). Of bear-pair associations considered, 24.8% were between male and female bears in pre-berry season.

The Fisher exact test was not sensitive to cutoff distance for positive associations, with the median probability staying close to 0 for paired times of <1 hr and 4,000 m for paired time separations >1 hr. The range of probabilities increased with cutoff distance, suggesting

Table 1. Frequency and percent of significant positive associations between grizzly bears from GPS collar data in west-central Alberta, Canada, 1999–2003.

Season Sex	Frequencies			Number of bear pairs	
	<1 hr ^a	>1 hr	Total	<i>n</i> ^b	% of <i>n</i> ^c
<i>Pre-berry season</i>					
Female–female	2	2	4	71	5.6
Male–female	23	13	36	145	24.8
Male–male	3	3	6	48	12.5
<i>Berry season</i>					
Female–female	5	3	8	50	16.0
Male–female	4	7	11	75	14.7
Male–male	1	2	3	15	20.0

^aDifference in reporting times between paired GPS locations.

^bBear pairs with home range overlap >0.

^cPercent bear pairs sampled that had significant associations.

Table 2. Number of active collars and sex composition of grizzly bear associations used in individual bear-pair analysis in west-central Alberta, Canada, 1999–2003. Numbers in parenthesis indicate unique bear-pairs.

Sex composition	1999	2000	2001	2002	2003	Total
Male–female	10 (7)	25 (13)	8 (4)	15 (10)	13 (7)	71 (41)
Female–female	13 (1)	2 (2)	9 (3)	3 (3)	3 (2)	30 (11)
Male–male	3 (2)	1 (1)	0 (0)	3 (3)	2 (2)	9 (8)
Total	26 (10)	28 (16)	17 (7)	21 (16)	18 (11)	110 (60)
Number of active collars	13	21	21	24	33	112
GPS locations	6,051	9,008	11,652	8,728	11,336	46,775

that only a small number of association tests may have been sensitive to cutoff distance. For example, only 8 of 68 associations that were significant at the 500 m cutoff were non-significant when evaluated at 2,000 m. Of these, 3 were from bears with time pairings of <1 hr and 5 were from bears with time pairings of >3 hrs. This suggests that positive association extends to greater distances than 500 m. The median *P*-value remained <0.05 for distances <10,000 m, suggesting overall test robustness to the 500 m cutoff. The observed effect of paired separations of >1 hr was increased variance and uncertainty in test outcomes as a function of cutoff distance. However, the median probability value remained low, suggesting overall test robustness. The main conclusion from sensitivity analysis is that bears seldom are close unless they are associating in some way. Sensitivity analysis for negative associations was not pursued because none was detected at 500 m.

Individual bear-pair analysis

During 1999 to 2003, a total of 110 bear associations met the selection criteria to obtain the best possible location data with reference to time. These associations involved 55 unique bear pairs made up of 40 individuals (Table 2). Of the 55 unique bear pairs, 38 were MF and 17 were of the same sex. Three MF bear pairs and 2 same-sex pairs associated in more than 1 year.

Genetics. Of the 55 unique bear pairs, 2 were parent–offspring and 2 were sisters. No remaining unique bear pairs fit our criteria for parent–offspring or siblings with the possible exception of one MF association. We did not obtain an age for one male who associated with a 21-year-old female in 2000 and a 13-year-old female in 1999. This male matched with these 2 females at 12 and 11 alleles respectively, so it is possible that this male was a littermate with one of these females.

Table 3. Number of partners per grizzly bear (p/b) by year and sex in west-central Alberta, Canada, 1999–2003.

Year	Male			Female		
	bears	partners	p/b	bears	partners	p/b
1999	4	7	1.8	5	7	1.4
2000	6	13	2.2	10	13	1.3
2001	2	4	2.0	4	4	1.0
2002	5	10	2.0	9	10	1.1
2003	6	7	1.2	5	7	1.4
All years	23	41	1.8	33	41	1.2

Of the 2 parent–offspring associations, one occurred on 25 June 2002 between an 18-year-old father and his 12-year-old daughter and lasted no more than 4 hrs. The other occurred between a mother and her 2-year-old daughter shortly after we collared the 2-year-old. Additionally, during relocation flights, these 2 female bears were seen together throughout the spring, summer, and fall. A pair of 5-year-old sisters associated 4 times in the pre-berry season and 9 times in the berry season in 1999 and 3 times in the pre-berry season and 4 times in the berry season in 2001. The other pair of sisters was older (11 yrs old in 2000) and associated for 52 hrs in mid August.

Age and sex. There was no significant difference ($t = 0.41$, 53 df, $P = 0.7$) in the mean age of females (8.1 yrs, $n = 31$, SE = 0.8) and males (8.6 yrs, $n = 24$, SE = 1.0) in MF associations. The mean age of females in the FF associations (7.9 yrs, $n = 19$, SE = 1.1) was also not significantly different ($t = 0.13$, 30 df, $P = 0.9$) from the mean age of males in MM associations (7.8 yrs, $n = 13$, SE = 1.2) or from the mean female age in the MF associations ($t = -0.11$, 48 df, $P = 0.9$).

Sixty-six percent of MF associations consisted of adult males and adult females. Subadult females were involved in 18% of the associations involving adult males. Nineteen percent of all MF associations involved subadult males. In same-sex associations, 55% of FF and 63% of MM associations consisted of adult animals. Male bears overall had associations with more partners per year than females ($U = 3.00$, $n_1 = 5$, $n_2 = 5$, $P < 0.05$; Table 3).

Timing. The latest association of any kind was a FF association on 25 October 2002 (Fig. 3). The earliest MF association detected was 14 May 2002 and the latest was 20 September 2003 (Fig. 4). Although MF associations occurred in most months, significantly more (79%) of the MF associations occurred between mid May and the end of July ($\chi^2 = 23.73$, 1 df, $P < 0.05$). MM associations occurred twice as often in the pre-berry season than in the berry season, whereas FF associations occurred more frequently in the berry season (Fig. 5).

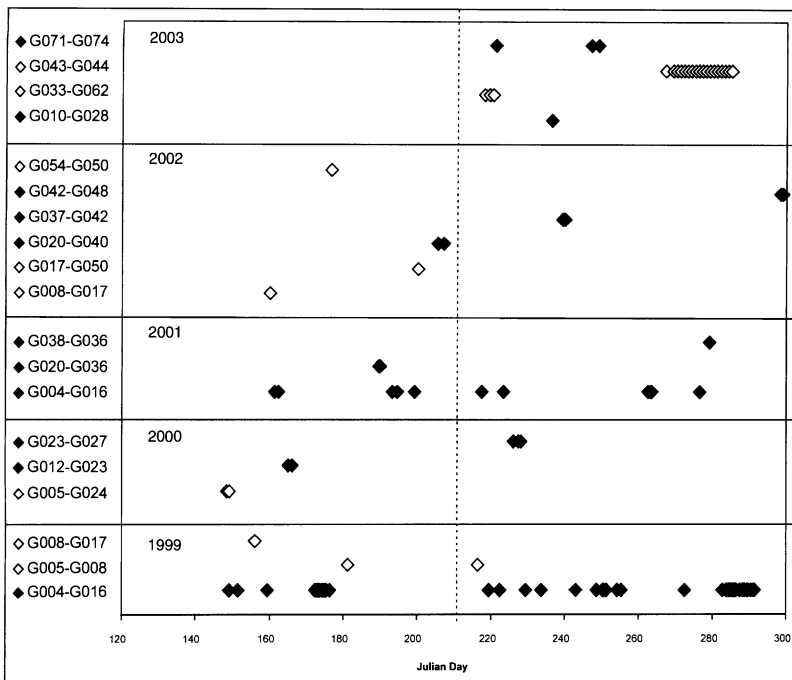


Fig. 3. Association of collared male-male (◇) and female-female (◆) grizzly bears in west-central Alberta, 1999–2003. The dashed vertical line separates pre-berry season from berry season.

Duration. MF associations varied in length from no more than 2 hrs to a maximum of 468 hrs with a mean of 59.9 hrs ($n = 71$, $SE = 10.2$). When 2 outlying associations that exceeded 400 hrs were excluded, 72% of MF associations lasted <72 hrs. The mean duration of MF associations in the pre-berry season (73.3 hrs, $SE = 9.8$, $n = 56$) was significantly longer ($U = 222.00$, $n_1 = 15$, $n_2 = 56$, $P < 0.05$) than in the berry season (10.3 hrs, $SE = 2.4$, $n = 15$). The mean duration of MF associations involving adult females in the pre-berry season was not significantly different from those involving subadult females ($U = 326.50$, $n_1 = 43$, $n_2 = 13$, $P = 0.35$). The number of associations in the berry season was too small to allow analysis of differences within age classes.

The mean duration of MM associations was longer than FF, but the difference was not significant ($U = 159.00$, $n_1 = 30$, $n_2 = 9$, $P = 0.44$) (Table 4). There were 2 associations that were substantially longer than all others and included a FF association that involved known siblings and a MM association that involved 2 bears of the same age. These bears may have been siblings; however, determination of this family relationship was not conclusive. When these outliers were excluded from the analysis, the mean duration of FF (22 hrs, $SE = 2.6$, $n = 52$) and MM associations (13.8 hrs, $SE = 8.0$, $n = 8$)

was still not significantly different. However, the mean duration of same-sex associations was significantly shorter than MF associations ($U = 1719.00$, $n_1 = 71$, $n_2 = 39$, $P = 0.03$).

Fifty-one percent of MF pairs associated more than once in a single year (multiple associations). The mean length of the first association in multiple MF associations (59.3 hrs, $n = 21$, $SE = 14.9$) was not significantly different ($U = 185$, $n_1 = 21$, $n_2 = 20$, $P = 0.51$) from single associations (69.7 hrs, $n = 20$, $SE = 79.7$). Although the mean length of the first 2 associations of a multiple association were almost twice that of the third and fourth, this difference was not significant ($U = 91.50$, $n_1 = 26$, $n_2 = 6$, $P = 0.51$).

Not all associations were continuous, as some bears were not within 500 m of each other through the complete span of an association. For those associations represented by more than a single point, 20 of 47 (43%) were discontinuous (contained more than 1

pairing). The mean duration of discontinuous associations, 150.2 hrs ($n = 20$, $SE = 23.3$), was significantly greater than continuous associations (43.2 hrs, $n = 27$, $SE = 9.2$; $U = 476.00$, $n_1 = 20$, $n_2 = 27$, $P < 0.01$).

Pairings and intervals. Pairings were defined as that time in which bears were continuously <500 m apart. Some associations consisted of a single pairing. We only used associations in which the time interval between GPS recordings was <0.6 hrs to examine the duration and frequency of pairings. With this criterion, pairings occurred only during May and June. The number of pairings per association ranged from 1 to 6 with a mean of 1.6 ($n = 20$, $SE = 0.3$). The distance apart during pairings ranged from 0 to 494 m with 86.8% under 250 m. The duration of those pairings ranged from ≤ 2 hrs to 198 hrs with a mean of 52.7 hrs ($n = 31$, $SE = 10.7$). The duration of the corresponding intervals between pairings ranged from 4 to 36 hrs with a mean of 7.3 hrs ($n = 11$, $SE = 2.9$). Intervals by definition were >500 m; however, the maximum distance apart during an interval did not exceed 1151 m.

Separation distances, rates of movement, and directional index. We investigated the mean rates of movement (ROM) of individual bears before, during, and after an association (Fig. 6). Because the

difference in acquisition time between bears in a pair directly affects the determination of both the distance separating the bears and the directional index, only bears with time differences of <0.6 hrs were included in these calculations. However, the calculation of rates of movement for individual bears is independent of the difference in acquisition time. Consequently, all bears were used in ROM calculations.

During MF associations, the mean distance apart was 151.9 m (SE = 11.8, $n = 249$) and varied from 0 to 1,151 m. Eighty three percent of paired locations were <250 m apart. The mean distance separating a bear pair during the approach and departure periods was considerably greater than during an association. Although not unexpected, this illustrates that bears did not remain stationary prior to or after an association.

The mean rates of movement of both males ($F = 13.85$; 2,189 df, $P < 0.01$) and females ($F = 6.62$; 2,185 df; $P < 0.01$) were significantly affected by the phase of an association. Both approach and departure were characterized by a mean movement rate higher than the rate during the association. The directional index was also significantly higher ($H = 11.05$, $n_1 = 11$, $n_2 = 17$, $n_3 = 15$ df, $P < 0.01$) during the association phase than the approach or departure phases, indicating a more similar direction of movement during the association. Males had a faster rate of movement prior to and after an association than did females.

Discussion

We concluded from our population analysis that bears with overlapping home ranges were seldom close unless they were associating in some way. This suggests that behavioral factors may play a significant role in bear positioning and movements, a factor that is ignored in most habitat selection models. For example, of 145 male and female GPS collared bears with home range overlap, 24.8% were associating in the pre-berry season (Table 1). From the individual bear-pair analysis, the average duration of MF associations during the pre-berry season

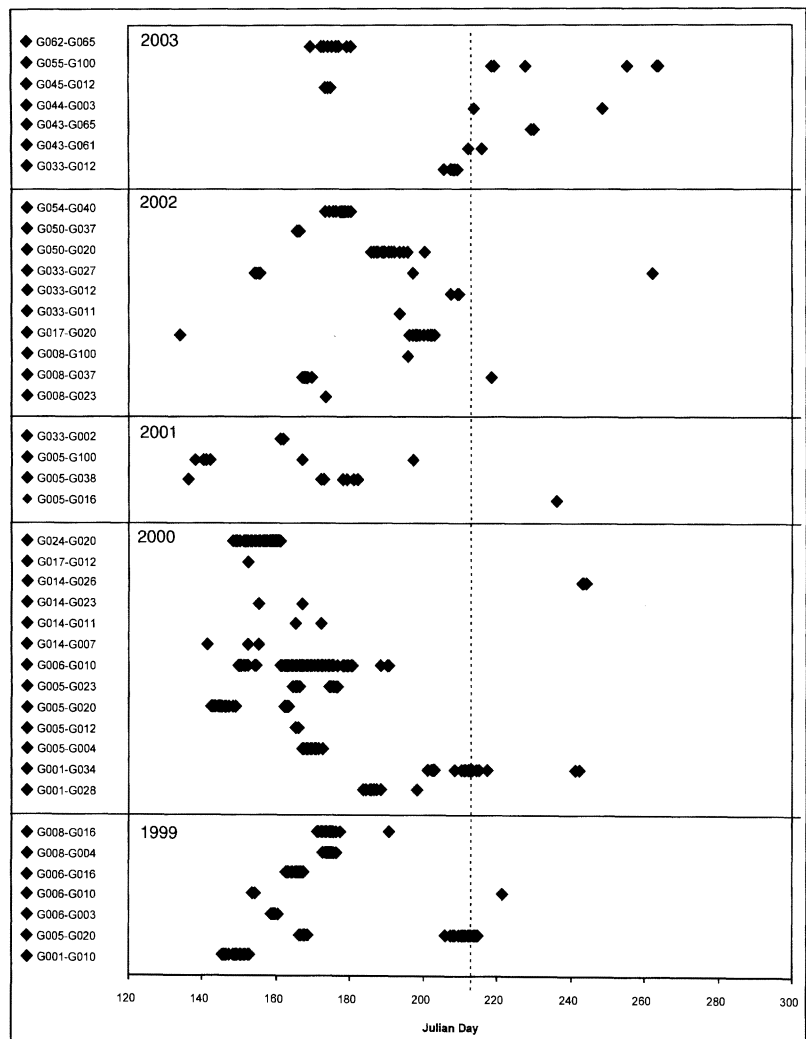


Fig. 4. Association of collared male–female grizzly bears in west-central Alberta, Canada, 1999–2003. The dashed vertical line separates pre-berry season from berry season.

was 73.3 hrs, suggesting that association played a significant role in bear positioning and movement at that time of year. One of the assumptions of habitat selection analyses is that bears behave in an independent fashion and their distribution is habitat based. An association between bears violates this assumption. Thus, knowing the proportion of the population that may be associating should be of interest to biologists inferring habitat selection from telemetry data.

Minimal change in probabilities for positive associations occurring due to chance at moderate distances (4,000–6,000 m) suggests that associations detected at 500 m are robust to spatial and temporal variation in the exactness of paired points. It also suggests that small

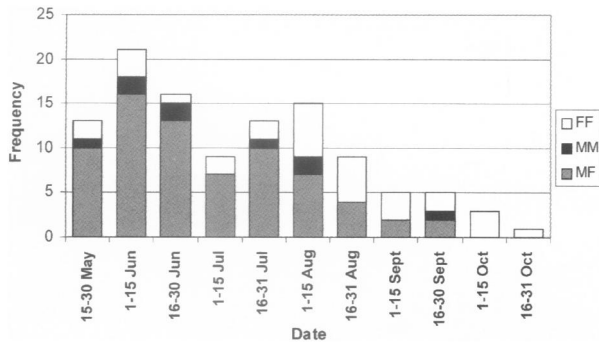


Fig. 5. Timing of grizzly bear associations in west-central Alberta, Canada, 1999–2003. FF = female–female pair, MM = male–male pair, MF = male–female pair.

scale errors in GPS locations and differences in paired reporting times should not substantially affect test results. The main effect of longer separations between reporting times was increased variance in test outcomes. The most conservative strategy would be to use only GPS acquisition times of <1-hr time separations. However, similarities in sex ratios with different time separations suggest similar outcomes in terms of positive associations when considered at the population level (Table 1).

Our results suggest that negative association of bears is not detectable at the 500 m cutoff and that avoidance behavior probably occurs at greater spatial scales. In addition, it highlights that this analysis can only test the probability of bears occurring close together, and behaviors such as aggression (a bear chasing another bear) could be detected as a positive association, further demonstrating that actual behavioral causation cannot be inferred from GPS points alone.

A potential problem with this analysis is autocorrelation of data points from bear movements sampled at 4-hr intervals, as discussed by Swihart and Slade (1985, 1997). Autocorrelation could inflate frequencies of spatially and temporally linked points due to non-independence of successive points. The effect of autocorrelation was partially tested by conducting the test at greater distance cutoffs. If a large degree of autocorrelation was present, the degree of significance would be reduced as distance cutoff increased (and the degree of spatial correlation between points decreased). In our study, the outcome of tests remained the same for the majority of bear pairs even when distance cutoff was increased to 2,000 m. This suggests the outcomes of tests were not greatly affected by autocorrelation of points.

The individual bear-pair level analyses provided further details on mutual attraction associations. Although

Table 4. Duration of grizzly bear associations in west-central Alberta, Canada, 1999–2003.

	Mean duration, hr	SE	<i>n</i>	Max
Male–female	59.9	10.2	71	468
Female–female	25.3	7.5	30	208
Male–male	58.9	45.7	9	420

our data cannot identify behaviors occurring between bears, it does support general findings of other grizzly bear behavioral studies. We showed that associations of the same and opposite sex occur in all seasons, but the majority of opposite sex associations happened in the pre-berry season and presumably involved breeding. We also showed that the majority of all MF associations involved neither parent–offspring nor littermates. The mating period, which includes pre- and post-copulatory behavior as defined by Craighead et al. (1969) for Yellowstone grizzly bears, extended from mid-May to mid-July, peaking in mid-June. Based on the frequency and duration of MF associations from our data, we believe the mating season in west-central Alberta to be slightly longer, lasting until the end of July and peaking in mid June.

During the mating season, male and female grizzly bears may form pair bonds lasting weeks or a few hours (Craighead et al. 1969, Herrero and Hamer 1977). This variability has been partly attributed to male grizzly bears using different strategies depending on age, experience, and size (Hornocker 1962, Craighead et al. 1969). Hornocker (1962) concluded that a well-established pecking order existed among sexes in Yellowstone National Park. The dominant male bear actively defended a female prior to and during her estrus period, while the lower ranked male bears attempted to mate with as many females as possible, especially in the absence of more dominant male bears. In our study, the majority of males visited >1 female during the breeding season; however, one 17-year-old collared male associated with only 1 collared 14-year old female during the entire mating season. Although we cannot be sure the male did not visit any uncollared females or the female did not associate with any uncollared males, we believe this is an example of a male defending a female.

The occurrence and duration of a MF association during the mating period will also be influenced by the female’s estrous period. Craighead et al. (1969) found that a female’s estrous period can be brief (1 day) or extended (27 days) and that some female grizzlies will have 2 estrous cycles during a mating season. Associations during the mating season in our study ranged from 4 hr to

468 hr, and we had several instances of females with 2 long associations in the mating season, suggesting that more than 1 estrous period may have occurred.

Although sample sizes were small, our data show that same-sex associations occurred. Excluding sibling associations, >50% of the FF associations involved an adult with a subadult. Because the Doncaster test filtered out associations due to chance, there must have been reasons these bears were near each other, but lacking direct observational behavior data, they remain unclear. With the exception of one long MM association that occurred in the berry season, MM associations were typically short (<8 hrs). We suspect some of the MM associations that occurred in the mating season were likely a result of an uncollared female in the area and attracting nearby males.

Males exhibited a faster rate of movement prior to and after an association than females. This is likely an important behavioral trait for males of a promiscuous species with large home ranges. Because a female's estrus period is variable in length and may occur more than once in a season (Craighead et al. 1969), a male would increase his odds of mating if he were to visit as many females as possible. To do this a male grizzly bear must likely cover long distances, and the faster he moves, the more females he can visit. Thus any effect on a male's ability to move across the landscape could have a detrimental effect on the reproductive potential of the population. This effect will be greatest for low density populations where the number of partners per bear is already low. Our data suggested that the majority of male grizzly bears in west-central Alberta were visiting >1 female more than once during the mating season. Thus, any reduction in the ability of male grizzly bears to move across the landscape in west-central Alberta could detrimentally affect the social behaviors and ultimately the reproductive potential of this population.

The new technologies of GPS telemetry and DNA analysis provided a unique opportunity to investigate associations between grizzly bears in a portion of their range in Alberta and suggested that the behavioral interactions between grizzly bears are more complicated than what we may believe or currently understand. In the past,

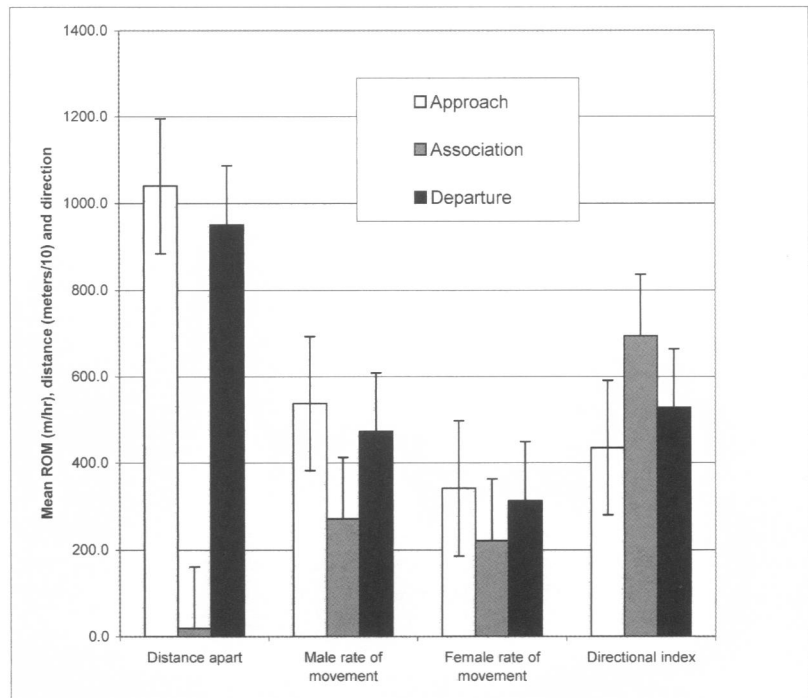


Fig. 6. Mean distances apart, rates of movements (ROM), and directional index during approach, association, and departure phases of male–female associations in west-central Alberta, Canada, 1999–2003. Distance and directional index have been adjusted to fit on same scale as ROM. Bars represent standard error.

these general life history questions have often been limited to direct observation. Although the effects of uncollared bears within the study area on associations are unknown, we believe our data provides new insights into this aspect of grizzly bear behavior and represents the best information available on this topic. A number of other parameters may influence grizzly bear associations, such as weather, seasonal food response, prey density and distribution, and grizzly bear density and distribution, but it was beyond the scope of our investigation to delve into these. Nevertheless, we acknowledge and advise other biologists and managers to be aware of the complexity of grizzly bear associations and consider them when constructing habitat use models.

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Literature cited

- AGRESTI, A. 1990. Categorical data analysis. John Wiley and Sons, New York, New York, USA.
- CATTET, M.R.L., K. CHRISTISON, N.A. CAULKETT, AND G.B. STENHOUSE. 2003a. Physiologic responses of grizzly bears to different methods of capture. *Journal of Wildlife Diseases* 39:649–654.
- , N.A. CAULKETT, AND G.B. STENHOUSE. 2003b. Anesthesia of grizzly bears using xylazine–zolazepam–tiletamine or zolazepam–tiletamine. *Ursus* 14:88–93.
- CLEVINGER, A.P., F.J. PURROY, AND M. SAENZ DE BURUAGA. 1992. Copulation of wild European brown bears (*Ursus arctos*) with comments on the breeding behaviour of one adult male. *Mammalia* 56:1–8.
- CRAIGHEAD, J.J., M.G. HORNOCKER, AND F.C. CRAIGHEAD. 1969. Reproductive biology of young female grizzly bears. *Journal of Reproduction and Fertility Supplement*. 6:447–475.
- DONCASTER, C.P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* 143:431–443.
- GIBEAU, M.L. 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. Dissertation, University of Calgary, Calgary, Alberta, Canada.
- HERRERO, S., AND D. HAMER. 1977. Courtship and copulation of a pair of grizzly bears, with comments on reproductive plasticity and strategy. *Journal of Mammalogy* 58:441–444.
- HORNOCKER, M.G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. Thesis, Montana State University, Missoula, Montana, USA.
- KOENE, P., J. ARDESCH, A. LUDRIKS, E. URFF, L. WENZELIDES, AND V. WITTENBERG. 2002. Interspecific and intraspecific social interactions among brown bears and wolves in an enclosure. *Ursus* 13:85–93.
- MACE, R.D., AND J.S. WALLER. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *Journal of Wildlife Management* 61:39–52.
- MUNDY, K.R.D., AND D.R. FLOOK. 1964. Notes on the mating activity of grizzly and black bears. *Journal of Mammalogy* 45:637–638.
- NAGY, J.A., A.W.L. HAWLEY, M.W. BARRETT, AND J.W. NOLAN. 1989. Population characteristics of grizzly and black bears in west-central Alberta. Alberta Environmental Centre, Edmonton, Alberta, Canada.
- PAETKAU, D., AND C. STROBECK. 1994. Microsatellite analysis of genetic variation in black bear populations. *Molecular Ecology* 3:489–495.
- PEARSON, A.M., AND J. NOLAN. 1976. The ecology of the grizzly bear in Jasper. The Canadian Wildlife Service, Ottawa, Canada.
- RUSSELL, R.H., J.W. NOLAN, N.G. WOODY, AND G.H. ANDERSON. 1979. A study of the grizzly bear in Jasper National Park, 1975 to 1978. Canadian Wildlife Service, Ottawa, Canada.
- SAS INSTITUTE. 2000. The SAS System for Windows. Version 8.1. The SAS Institute, Cary, North Carolina, USA.
- SWIHART, R.K., AND N.A. SLADE. 1985. Testing for independence of observations in animal movements. *Ecology* 66:1176–1184.
- , AND ———. 1997. On testing for the independence of animal movements. *Journal of Agricultural, Biological, and Environmental Statistics* 2:48–63.
- WIELGUS, R.B., AND F.L. BUNNELL. 1994. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405–416.
- , AND ———. 1995. Test of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59:552–560.
- WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

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