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Grizzly bear space use, survival, and persistence in relation to human habitation and access

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Abstract: Previous studies showed that the likelihood of a bear becoming a nuisance and thus being removed from a population (i.e., relocated or killed) depends on numerous factors such as natural food supply, sex, age, and reproductive status. Distances from a bear's home range and activity centers to conflict zones such as towns, roads, and trails used by humans also affect the incidence of nuisance behavior and have been documented for grizzly/brown bears (*Ursus arctos*) in North America and Europe. But those studies did not quantify the relative influences by various factors on distance from conflict zones, or the effects of distance on the likelihood of becoming a nuisance. We tested the latter 2 aspects using data gathered for other purposes on 9 adult research grizzly bears using areas within 500 m of Cadomin, Canada, during an 8-year study between 2000 and 2010. GPS radio collars yielded 565 location positions, of which 87% (490) were for 3 females. Bear distances to the settlement varied mostly as a function of seasonal natural food supply and foraging intensity (spring hypophagia, summer mesophagia, and fall hyperphagia); distances were less a function of sex, reproductive status, age, day of the week (proxy for high human presence), or individual differences. However, females occurred disproportionately more than males (92%) in a 500-m radius from town. Bears were closest to Cadomin in spring and fall, but feeding and bedding activity occurred within 500 m of the settlement across seasons. By contrast, bear distances from roads and trails differed less as a function of season than they did among individuals, but that revealed nothing about nuisance potential. Adult female G040, the single research bear that became a problem because it entered the settlement and foraged there, did not tend to be closer to roads and trails than most bears. During the year that G040 visited Cadomin, her average distance from that settlement ($\bar{x}$ ± 2 SE: 281 ± 51 m, n = 37) was not closer than distances of the other bears to Cadomin (303 ± 11 m, n = 512), although it was closer than her mean distance during the 2 other years on which we have data (387 ± 90 m, n = 10). Based on these findings and bear-related occurrences reported by residents, we conclude that seasonal and annual deficits of prime natural foods, and availability of anthropogenic foods, remain the best predictors of nuisance activity for bears in general.

Key words: conflict, fitness, individual variation, nuisance wildlife, problem animal, roads, trails, *Ursus arctos*

Growing human populations and expansion of human settlements and roads into wilderness areas are expected to increase the likelihood of human–wildlife interactions (Trombulak and Frissell 2000, Woodroffe 2000, Treves and Karanth 2003, Distefano 2004). Such interactions can result in complex human–wildlife system dynamics along gradients of wildlife habituation and tolerance of and by humans (Samia et al. 2015), which can affect wildlife population persistence and potentially incur safety risks to humans and property (Smith et al. 2005). Understanding factors that might predispose animals to becoming a nuisance and how individuals vary in susceptibility to nuisance behavior could facilitate damage prevention. Furthermore, elucidating behavioral variation among individuals as well as among age and sex classes can inform conservation and management of wildlife populations (Blumstein and Fernandez-Juricic 2004, Caro 2007, Caro and Sherman 2011, Cristescu and Boyce 2013). Yet for large mammalian species that come into conflict with people, field settings present

Figure 1. Grizzly bear captured and removed from Cadomin that survived and had her own cubs following translocation. (*Photo by Amy Stenhouse*)

unique challenges as individuals cover wide ranges, often in rugged or densely vegetated landscapes where monitoring is difficult.

Bears are a classic example of large-bodied mammals increasingly exposed to anthropogenic factors and thereby susceptible to conflict with humans (Peine 2001, Can et al. 2014). Human–bear conflict has been documented for all extant bear species, including American black bears (*Ursus americanus*; Spencer et al. 2007), Asiatic black bears (*U. thibetanus*; Charoo et al. 2011), brown bears (Mattson and Merrill 2002), polar bears (*U. maritimus*; Dyck 2006), sloth bears (*U. ursinus*; Bargali et al. 2005), spectacled bears (*Tremarctos ornatus*; Goldstein et al. 2006), and sun bears (*U. malayanus*; Wong et al. 2015), as well as giant panda (*Ailuropoda melanoleuca*; Liu et al. 1999). Bear habituation to humans—defined as the waning of a flight response when a punishment (e.g., non-lethal deterrent) is discontinued (adapted from McCullough 1982, Hopkins III et al. 2010)—can lead to human–bear conflict (Smith et al. 2005). Relatedly, low human tolerance of bears wherein tolerance represents the intensity of bear disturbance that a person tolerates without responding negatively (adapted from Nisbet 2000, Hopkins III et al. 2010) can also result in conflict.

Human–bear interactions are relatively rare in North America; grizzly bears have been involved in more incidents that resulted in serious injuries to people than have black or polar bears (Herrero and Fleck 1990). As the largest terrestrial carnivore on the continent, the grizzly bear once ranged across most of the central and western regions, but current distribution is greatly reduced because of human persecution and habitat loss (Laliberte and Ripple 2004, Proctor et al. 2012). With human settlements and access increasingly expanding into bear habitats, human-caused mortality of grizzly bears is likely to increase (Noss et al. 1996, McLellan 1998, Nielsen et al. 2004*b*, Boulanger and Stenhouse 2014). Conflict mitigation might be facilitated if one could identify factors that predispose carnivores to conflict with people (Linnell et al. 1999).

A wealth of information exists on grizzly bear food habits (Jacoby et al. 1999, Mowat and Heard 2006, Munro et al. 2006, Edwards et al. 2011, Cristescu et al. 2015*a*), habitat selection (Blanchard 1983, Nielsen et al. 2003, Ciarniello et al. 2007), movements (Boyce et al. 2010, Roever et al. 2010, Proctor et al. 2012) and population dynamics (Shaffer 1983, Boyce et al. 2001, Wielgus 2002). Recently, Elfström et al. (2014) investigated several factors that might determine bear use of areas near human habitation, proposing that bears near settlements should not be considered "unnatural," but rather exhibiting adaptive behavior as a reflection of despotic distribution among conspecifics. By contrast, how individual variability influences bear survival, persistence, and reproductive success in relation to human settlements and access remains largely unknown.

Roads and trails increase the chance of human–bear encounters and mortality risk for bears (Benn and Herrero 2002, Nielsen et al. 2004*b*) by direct vehicular traffic, sport hunting, poaching, or self-defense killing of bears that threaten or attack someone during a surprise encounter. In North America, whether a problem bear is killed or relocated sometimes depends on a government response protocol that considers age, sex, and reproductive status, along with the bear's known history of past conflicts and conflict type. While grizzly bears that come into direct contact with or attack humans are often destroyed by

Table 1. Grizzly bear GPS radio collar data recorded within 500 m of Cadomin, Alberta, Canada during 2000–2010.

Bear status	Bear ID	Sex	Number of locations					
			Hypophagia	Mesophagia	Hyperphagia	Weekend	Total	# years of monitoring
Research	G023	Female	28	3	196	64	227	6 (6)[c]
	G029[a]	Male	1	0	0	0	1	4 (1)[c]
	G037[a]	Female	0	0	1	0	1	3 (1)[c]
	G040[b]	Female	0	0	10	3	10	3 (2)[c]
	G055	Male	4	4	7	2	15	1 (1)[c]
	G111	Female	7	24	0	7	31	3 (3)[c]
	G112	Male	23	0	0	0	23	1 (1)[c]
	G113	Female	56	99	61	77	216	2 (2)[c]
	G115[a]	Male	0	1	0	1	1	2 (1)[c]
Problem	G040[b]	Female	19	18	0	1	37	1 (1)[c]
	378615[a]	Male	2	0	0	0	2	N/A
	380139[a]	Male	0	0	1	0	1	N/A
All bears	All bears[d]	Male & Female	140 (137)	149 (148)	276 (274)	154 (153)	565 (559)	26 (19)[c]

[a] Locations excluded from analyses because of small sample size
[b] Research bear wearing collar becoming problem animal in mesophagia. Bear was subsequently captured and relocated by Alberta ESRD
[c] Number of monitoring years. In brackets, number of years with occurrence within 500 m of Cadomin
[d] Total number of GPS locations within 500 m of Cadomin. In brackets, number of locations used in statistical analyses

regulatory agencies, those problem individuals entering human settlements, feeding on human foods, destroying property, or depredating on livestock are usually given a second chance by capture and translocation (Figure 1). While avoiding immediate mortalities, many relocations are unsuccessful, resulting in new conflicts and/or bear deaths in the area where translocation occurred (Riley et al. 1994, Blanchard and Knight 1995). Because bears may move away temporarily from the conflict site, bears captured as part of human–bear conflict management are not always the guilty individuals. Preventing problems is preferable and more successful than trying to cure them, as the problem animal designation requires detailed understanding of bear behavior and mechanisms leading to conflict (Riley et al. 1994, Gunther et al. 2004).

We used an area in west-central Alberta, Canada with high human–bear conflict potential and a long-term bear monitoring program in place to inspect differences in space use among grizzly bears in relation to human habitation and access to address 2 goals: (1) to obtain field data to identify factors that increase or decrease a bear's likelihood of surviving in a habitat adjacent to a permanent human settlement, and (2) to use bear occurrence data for tailoring conservation strategies to better reduce and ideally prevent human–bear conflicts.

Material and methods

Study area

During 2000–2003, 2006, and 2008–2010, a 10,000-km^2 area centered on the Hamlet of Cadomin (hereafter, Cadomin), west-central Alberta, Canada was used for a broader study on grizzly bear response to open-pit mining development and reclamation (Stevens and Duval 2005, Cristescu 2013). Data collected in this study also provided a unique opportunity to investigate grizzly bear behavior in relation to Cadomin, which was classified as a high human–bear conflict area in a hazard assessment performed by the Alberta Government (AESRD 2010). This small rural community is relatively isolated from other permanent settlements, with the nearest inhabited centers at distances of 39 km (Robb; 2006: population = 186) and 57 km (Hinton; 2006: population = 9,738; Statistics Canada 2013).

While Cadomin is now sparsely populated (2006: population = 56; Statistics Canada 2013), it reached 2,500 in the 1950s, during widespread coal mining in the region (YC 2012). Today open-pit mining is still a major land use near Cadomin, but most mine employees commute daily to other nearby towns where they reside. Unlike many other rural settlements in Alberta with growth rates tied to natural resource commodity prices, Cadomin's spatial expansion is largely because of its appeal for outdoor recreational opportunities (YC 2012). Its population fluctuates seasonally, peaking in summer, fall, and on weekends.

Using an aerial orthophoto with 0.5-m precision, we delineated a polygon around Cadomin and created a series of concentric bands at 100-m increments radially out from Cadomin, up to 500 m (Figure 2). A few scattered houses were outside the 500-m band encompassing our study area.

Data sources

We compiled all available data on grizzly bear occurrence within 500 m of Cadomin during the study period. Our data were on research bears captured by the Foothills Research Institute's Grizzly Bear Program and University of Alberta, with supplementary data coming from problem bears captured by Alberta Government personnel. Two unbaited camera traps (Bushnell Trophy Cam; Overland Park, KS, USA) near the settlement (d_1 = 258 m; d_2 = 390 m) provided data on bear occurrence during 2010.

Grizzly bears were captured for GPS radio collar deployment (Advanced Telemetry Systems, Isanti, MN, USA; and Televilt, Lindesberg, Sweden) using helicopter darting, culvert traps and leg-hold snares. Protocols for research bears were approved by the University of Saskatchewan and University of Alberta Animal Care and Use

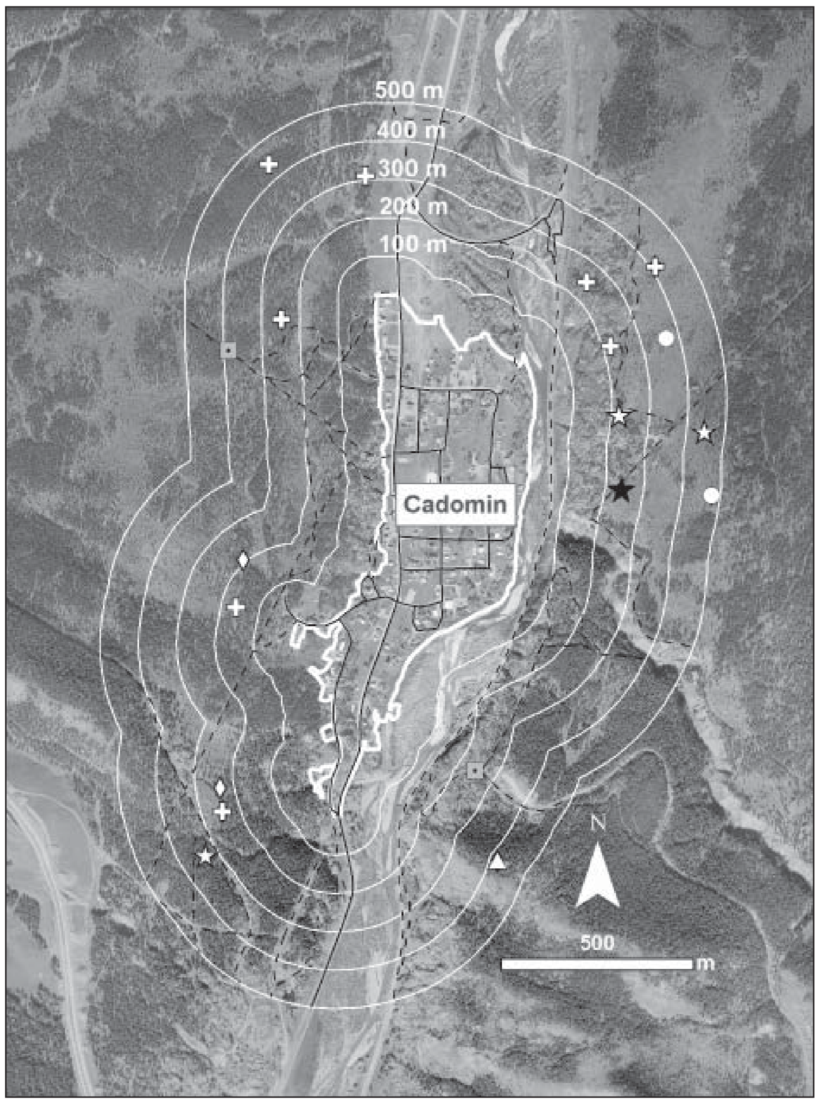

Figure 2. Study extent in Alberta, Canada, bounded by a 500-m buffer around Cadomin. Bear behaviors recorded during field visitation of GPS radio collar locations (2001–2003) and clusters (2008–2010) include ungulate consumption (white cross), bedding (white diamond), grazing (white triangle), root digging (white star), unknown digging (black star), and movement (white disk). Grey squares with center dots are camera trap locations. Cadomin extent is delineated by a thick white polygon, roads are in solid black, and trails are in dashed black.

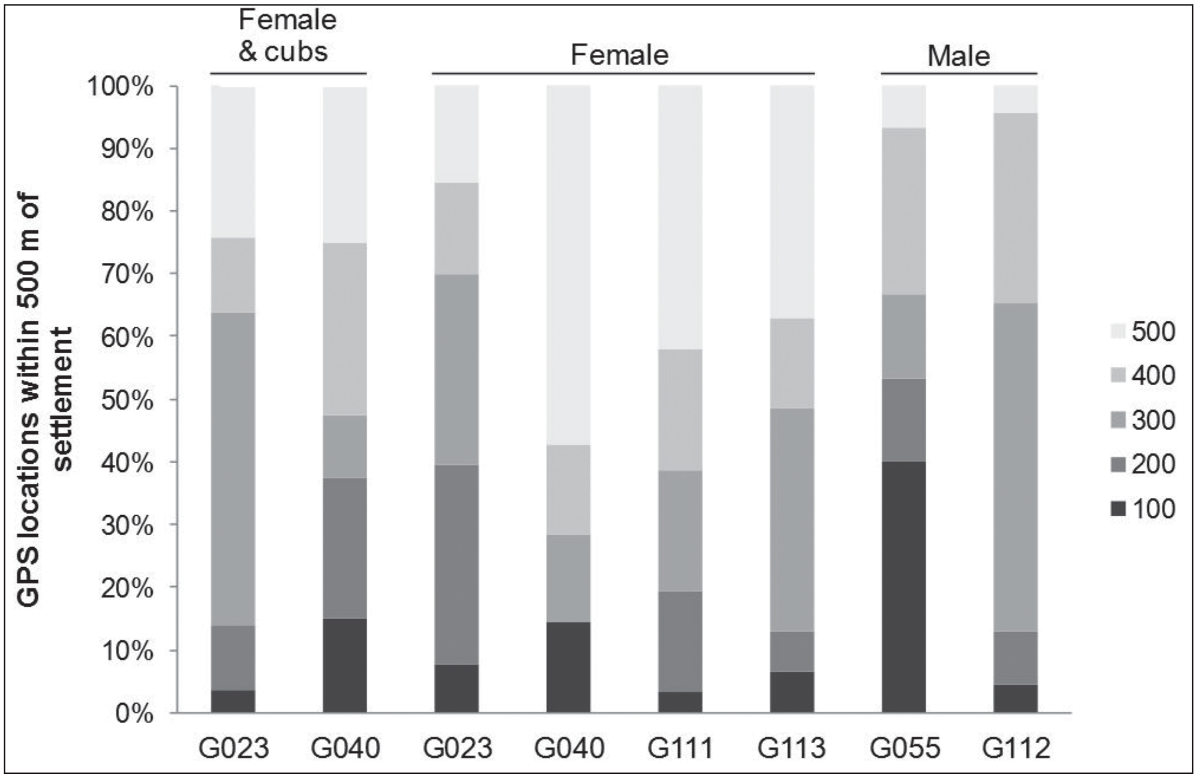

Figure 3. GPS radio collar locations within regular increment buffers (100 m) from Cadomin. Bear unique IDs are provided on the x-axis.

Committees, and protocols for problem bears were government regulated. Radio collars on research bears were programmed to acquire a location every 4 hours (2000–2003) and every 1 hour (2006 and 2008–2010). Radio collars on problem bears had less frequent and more variable relocation fixes. Bears were monitored for various amounts of time because of radio collar failure and large males sometimes slipping collars off prematurely.

In addition to monitoring movements, GPS data from research bears allowed field visitation of bear-use locations to record bear activity. From 2001 to 2003, selection of locations for field visitation occurred randomly from the GPS radio collar dataset, whereas from 2008 to 2010, selection was based on an algorithm modified from Knopff et al. (2009). The algorithm identified location clusters where the bear had spent ≥3 hours within a 6-day window, with initial cluster radius constrained to 50 m (Cristescu et al. 2015*b*).

Lastly, we obtained the 1999–2010 government database on public complaints related to grizzly bears occurring within the study area extent and inspected each record to obtain a validated list of conflicts occurring within 500 m of Cadomin. Conflicts were classified as minor (animal sightings) or major (any instance when a bear threatened human property or safety).

Statistical analyses

We used the bear GPS radio collar locations within the 500-m buffer (Table 1) to investigate differences in bear spatial occurrence in relation to Cadomin, roads, and trails receiving motorized and/or non-motorized human use. Distance values were extracted from 3 raster surfaces representing distance to Cadomin, roads, and trails, respectively. Values for bear-use locations were obtained by intersecting the raster grids at 30-m grain with bear-use locations. For each bear, we report the distribution of locations within buffered increments (Figure 3) as well as mean distances ($\bar{x}$) to Cadomin and human access routes (Figure 4; Appendix 1).

We formulated simple a priori hypotheses, which considered inter-individual variability, reproductive status, bear sex, bear age, season, and period of weekday to identify variables that

Table 2. Independent variables included in models for distance from bears to Cadomin, distance to road, and distance to trail.

Variable			
Name	Type	Units	Value
Individual	Categorical	N/A	G023 (23); G040 (40); G055 (55); G111 (111); G112 (112); G113 (113)
Sex	Categorical	N/A	Male (1); Female (2)
Reproductive status	Categorical	N/A	Male (1); Female (2); Female with cubs (3)
Age	Continuous	Years	2–22
Season	Categorical	N/A	Hypophagia (1); Mesophagia (2); Hyperphagia (3)
Weekend	Categorical	N/A	Saturday/Sunday and statutory holiday long-weekends (1); Monday–Friday (0)

could explain bear distance to Cadomin or roads and trails (Table 2). All variables were behaviorally relevant, as the first 4 variables represented intrinsic biological characteristics; seasonality was based on known feeding ecology of grizzly bears in the region. The seasonal division of data considered hypophagia (spring; den emergence to June 14), mesophagia (summer; June 15 to Aug. 7) and hyperphagia (fall; Aug. 8 to den entrance; Nielsen et al. 2004*a*).

We restricted the plausible hypotheses to 3 sets of eleven because of sample size limitations, collinearity issues at more complex variable combinations, and to adhere to the Burnham and Anderson model formulation philosophy (Burnham et al. 2011). Each hypothesis was tested using generalized linear models (GLM) in the gamma family distribution with an identity link, chosen because the factor variables were continuous but not normally distributed based on histogram inspection, tests of normality (Shapiro-Wilk: distance to Cadomin $W = 0.97$, $P < 0.05$; distance to road $W = 0.98$, $P < 0.05$; distance to trail $W = 0.84$, $P < 0.05$) and tests of skewness (all dependent variables: $P < 0.05$). A correlation test showed that variables included in hypothesized models with >1 variable were not correlated ($|r| < 0.7$). For all modeling procedures, we used robust standard errors to account for potential misspecification of the family distribution.

Models were ranked within each set using the difference in Akaike Information Criterion for small sample sizes (ΔAICc), wherein models with a ΔAICc <2 receive substantial support. We computed the percentage deviance explained by each model, to assess the extent to which tested variables could be used to explain the observed pattern of bear distances to Cadomin and human access. For the top model in each set, we assessed collinearity between predictors using variance inflation factors if the model included >2 variables. We tested the linearity of the response on scale of estimation using Pregibon's link test (Pregibon 1980). Finally, we correlated predicted and observed values of the dependent variable, with high correlations indicative of good predictive power (Zheng and Agresti 2000).

In addition, we investigated whether there were seasonal and weekday differences in bear frequency of activity within the study area extent, performing separate Fisher's exact tests for season, day of the week, and pooled feeding activity and bedding, respectively (as confirmed from GPS cluster visits). Because of small sample sizes, we carried out similar testing for pooled conflict occurrence frequency, but only in relation to season. Although we wanted to analyze conflict incidence by weekend versus weekday, we were unable to achieve this because only a small number of records had precise information on occurrence date.

Distance measurements, buffering, and variable extraction from GIS layers were carried out in ArcGIS 9.2, the Spatial Analyst extension and Hawth's Tools (Beyer 2007). All statistical modeling procedures were performed in STATA 11.2 (College Station, TX, USA). Fisher's exact test calculations were carried out in VassarStats (Lowry 2013).

Results

Cadomin bears

Nine adults of 55 bears captured in the 10,000-km^2 study region used areas within 500 m of Cadomin during the monitoring period ($n_{females}$ = 5; n_{males} = 4; Table 1). Of these, 3 bears had only 1 GPS location <500 m of the settlement and were excluded from analyses. Of the 4 females included in analyses, 2 females had cubs during a subset of the monitoring period. Bear G023 was accompanied by cubs during 5 of the 6 years of monitoring. Bear G040 had accompanying cubs in 2003 and 2006, but not 2002. She was trapped as a problem bear in 2006, when this family group began eating dog food in a Cadomin house backyard. This bear and her female surviving cub were relocated outside the bear population unit >190 km straight-line distance from the capture site; her second cub was found dead along a road near Cadomin. Two additional male problem bears as identified by Alberta Environment and Sustainable Resource Development (Alberta ESRD) used areas near Cadomin during the study period but were not included in analyses (Table 1). The 2 camera traps recorded 2 images of an adult (uncollared) grizzly bear in 2010, but we could not distinguish whether these were of the same individual, or if they were research or problem bears monitored in previous years. In addition, the cameras recorded images of black bears and wolves (*Canis lupus*). These data result in a conservative minimum estimate of 10 adult grizzly bears using the area near Cadomin during the 8-year monitoring period (Table 1). Our sample size for statistical modelling consisted of 6 bears (4 females and 2 males) that were monitored for a total of 26 bear-years ($\bar{x}$ ± SD: 2.9 ± 1.6 years), resulting in 559 GPS radio collar locations within 500 m of Cadomin. Home ranges of each of these 6 bears encompassed the entire study area extent.

Distance to Cadomin

The distribution of GPS radio collar locations within 100-m-wide bands around Cadomin differed between bears (Figure 3). Overall, bear distances from Cadomin averaged approximately 300 m ($\bar{x}$ ± 2 SE: 303 ± 11 m, *n* = 559). Distance averages for females with cubs were 300 ± 27 m (*n* = 98), lone females 308 ± 12 m (*n* = 423), and males 266 ± 38 m (*n* = 38). Four GPS locations occurred within Cadomin town limits: 2 locations by single female research bears (G113 in mesophagia; G023 in hyperphagia), and 2 locations by a female with cubs research bear that became a problem bear (G040 in hypophagia and mesophagia). The best predictors of distance from town were season and secondarily the weekly period (Table 3). Bears were closer to the settlement during hypophagia (301 ± 19 m, *n* = 137) and hyperphagia (268 ± 15, *n* = 274) than during mesophagia (372 ± 18, *n* = 148). They were also slightly closer on weekends (288 ± 18, *n* = 400) than during the rest of the week (310 ± 13, *n* = 159; Table 4).

Research bear G040 was on average 390 m from the settlement during 2002 and 2003 when she did not occur in the Cadomin town site (387 ± 90 m, *n* = 10), and closer in 2006 when she became a problem bear (281 ± 51 m, *n* = 37).

Distance to roads

Overall, bear locations occurred approximately 270 m from the nearest road (264 ± 11 m, *n* = 559). Females with cubs were 259 ± 28 m from the nearest road (*n* = 98), single females were 264 ± 13 m away (*n* = 423), whereas males were 267 ± 43 m away (*n* = 38). The only model that received substantial support included an individual bear as the single predictor variable for distance to roads (Table 3).

Distance to trails

Distance from the nearest human-use trail averaged 73 ± 6 m (*n* = 559) for all bears combined, being smallest for males (54 ± 16, *n* = 38), intermediate for females with cubs (67 ± 13 m, *n* = 98), and longest for lone females (75 ± 7 m, *n* = 423). Individual bear was again the best single predictor of distance. Considering season and weekly period only slightly improved predictability.

Model fit and prediction

Two of the 5 models that received substantial support included >1 variable, and we did not detect collinearity problems in either of them. Top models explained <1% of deviance and correlations between predicted and observed values of the dependent variables were low

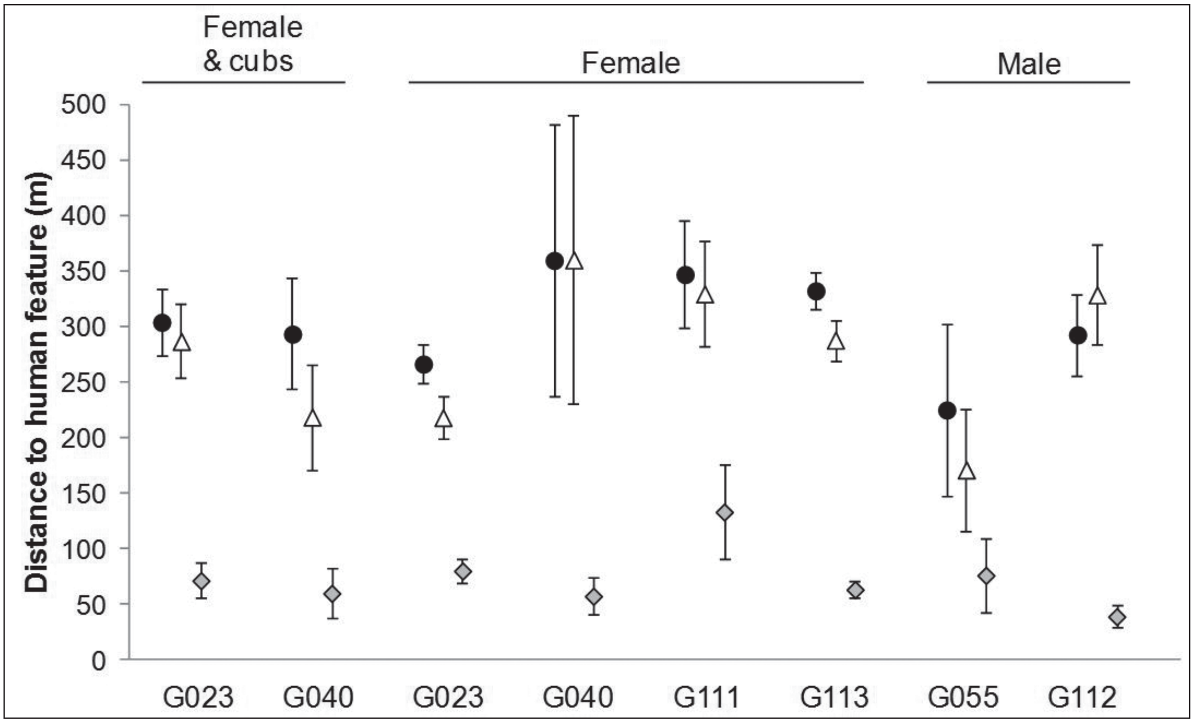

Figure 4. Distances from each bear to Cadomin, road, and trails, based on GPS locations acquired within 500 m from the settlement. Black circles represent mean distances to Cadomin, white triangles represent mean distances to roads, and grey diamonds represent mean distances to trails. Data are reported as means ± 2 SE.

($r < 0.35$ for all top ranked models). Based on these results and significant link tests for all top models, we conclude that additional variables and potentially larger sample sizes would be necessary to better predict factors influencing bear distances to Cadomin, roads, and trails. Although effect sizes as illustrated by percentage deviance explained were small, our models and information criterion framework did enable hypotheses ranking in relation to grizzly bear occurrence near human settlement, roads, and trails. Confidence intervals for several variables we tested did not overlap zero, suggesting that the respective variables were indeed associated with bear occurrence in relation to distances from settlement and human access routes.

Bear activity and reported conflicts

Five bear individual GPS locations and 12 GPS location clusters visited within 500 m of Cadomin had ungulate carcasses (n = 8), bear beds (n = 6), evidence of root digging (n = 3) and unknown digging (n = 1), herbaceous feeding (n = 1), and movement through the site (n = 2; Figure 2). Based on these data, there was no significant difference in feeding occurrence between seasons (Fisher's exact test, df = 2, P = 1.00) or by week day (Fisher's exact test, df = 2, P = 0.69), nor in bedding occurrence between seasons (Fisher's exact test, df = 2, P = 1.00) or by weekday (Fisher's exact test, df = 2, P = 1.00).

A total of 14 conflicts that could be confidently attributed to the study area were recorded during 1999–2010, with 11 conflicts being minor (bear sightings) and 3 conflicts being major according to our classification (bear did not leave backyard of private residence; bear ate dog food in dog kennel; bear attacked dog). There was no difference in conflict occurrence between seasons (Fisher's exact test, df = 2, P = 0.62).

Discussion

We took advantage of long-term space use data on a threatened population of grizzly bears to investigate the link between individual variability, survival, and persistence under the premise that humans can adversely affect wildlife populations through removal of individual bears as problem animals. During the course of the study, 1 monitored bear (G040, female with cubs) became accustomed to dog food set in the backyard of a Cadomin home. Translocation of this bear as a problem animal represented a milestone in this study. We viewed this undesired event as experimental manipulation, offering an opportunity to distinguish underlying behavioral patterns of space use by the problem bears and other bears in the area.

Bear distance to Cadomin was best explained by the seasonal and combined seasonal and weekend hypotheses. Seasonality, a proxy for food availability, explained more of the deviance than any other variable in univariate models. Bears were more likely to be closer to Cadomin during hypophagia and hyperphagia, and further in mesophagia when herbaceous material is widely available (Nielsen et al. 2010) and constitutes an important part of bear diet in the region (Munro et al. 2006, Cristescu et al. 2015*a*). Relatedly, grizzly bears in north-central British Columbia had the least use of anthropogenic foods during mesophagia when natural foods were most abundant (Wood and Ciarniello 2011). While American black bears also vary in their use of human food sources depending on season and natural food availability (Lyons 2005), individuals from some populations forage near and within human-inhabited areas even when availability of wildlands foods is high (Merkle et al. 2013). Although we had expected bears to be farther from town during weekends due to higher human numbers there and in surrounding forest, we found that bears were slightly closer to Cadomin on weekends. Bear movement may be influenced by increased within-settlement attractants during weekends, such as scents emitted by human foods. By contrast, bighorn sheep (*Ovis canadensis*) in California were temporarily displaced by higher numbers of humans on weekends (Longshore et al. 2013).

Although the bear sex variable was absent from supported models that considered a continuous distance metric for bear space use in relation to Cadomin, the sheer number of locations within 500 m of town that belonged to females (92% of all locations) speak to females using the area near the settlement more than males. This could potentially be indicative of habituation by these females and could explain why one of the females was deemed a problem bear. Brown and black bear females accompanied by cubs use areas near human settlements more than males and solitary females, probably to avoid potentially infanticidal males (Steyaert et al. 2013, Elfström et al. 2014). Based on our long-term data, female bears that have been reproductively successful still persist in the region and either feed on naturally occurring foods (G023) or avoid Cadomin (G037). By contrast, the female bear with cubs that became a problem animal (G040) was removed by Alberta ESRD in 2006 and thereby was unable to contribute offspring to the local population (1 cub was also removed and the other was found dead). Female bears that use urban areas are generally unable to realize their full reproductive potential because of higher mortality (or removal) compared to females in wilderness areas (Beckmann and Lackey 2008).

In other areas, sexual segregation can result in females using areas near roads as a refugia from males (McLellan and Shackleton 1988, Mattson 1990). The differential pattern we documented is possibly caused by the presence of bear grazing foods such as clovers (*Trifolium* spp.; Roever et al. 2008*a*) along roads and potentially trail sides, as well as the fact that gravel roads and trails have low human traffic (Roever et al. 2008*b*). Individual bears that maintain a large distance from roads, trails and Cadomin (e.g., female G111) may potentially do so in connection with previous negative experiences with humans. Nonetheless, even such bears are theoretically at potential risk of conflict with people, because all bears included in analyses had occurrences within 100 m of Cadomin (Figure 3).

The individual variability hypothesis received the most support in explaining bear distance to roads and trails. This result is in agreement with studies that underline the importance of incorporating individual variability into analyses of spatial occurrence and movement (Judson 1994, Hawkes 2009). The finding that individual variability outweighs other intrinsic biological characteristics adds to the results of studies that identify age, sex, or reproductive status as key intrinsic characteristics setting grizzly bears at risk of conflict with people (Maguire and Servheen 1992, Mattson et al. 1992, Riley

Table 3. Ranking of models explaining bear distance to Cadomin, distance to road, and distance to trail within a 500 m buffer from Cadomin. The top models based on ΔAICc ranking, which received substantial support (ΔAICc < 2) are shown in bold for each dependent variable.

	Distance to Cadomin						Distance to road						Distance to trail					
Hypothesis	K[a]	LL[b]	ΔAICc	w[c]	% D[d]	R[e]	K[a]	LL[b]	ΔAICc	w[c]	% D[d]	R[e]	K[a]	LL[b]	ΔAICc	w[c]	% D[d]	R[e]
Null model	1	-3753.68	8.5	0.01	0.00	9	1	-3675.24	7.9	0.01	0.00	7	1	-2953.61	25.6	0.00	0.00	12
Individual	2	-3750.86	5.1	0.03	0.08	7	**2**	**-3670.17**	**0.0**	**0.50**	**0.14**	**1**	**2**	**-2939.72**	**0.0**	**0.65**	**0.47**	**1**
Sex	2	-3753.35	10.1	0.00	0.01	11	2	-3675.24	10.1	0.00	0.00	12	2	-2952.03	24.6	0.00	0.05	11
Reproductive status	2	-3753.32	10.0	0.00	0.01	10	2	-3675.22	10.1	0.00	0.00	11	2	-2951.50	23.6	0.00	0.07	9
Age	2	-3751.55	6.5	0.02	0.06	8	2	-3671.17	2.0	0.18	0.11	2	2	-2951.42	23.4	0.00	0.07	8
Season	**2**	**-3748.31**	**0.0**	**0.42**	**0.14**	**1**	2	-3672.16	4.0	0.07	0.08	4	2	-2949.16	18.9	0.00	0.15	4
Weekend	2	-3753.38	10.1	0.00	0.01	12	2	-3674.99	9.7	0.00	0.01	10	2	-2951.73	24.0	0.00	0.06	10
Season + Weekend	**3**	**-3748.01**	**1.7**	**0.17**	**0.15**	**2**	3	-3671.97	5.9	0.03	0.09	6	3	-2948.33	19.6	0.00	0.18	5
Season + Weekend + Individual	4	-3746.93	2.0	0.15	0.18	3	4	-3669.0	2.5	0.15	0.17	3	**4**	**-2937.89**	**1.1**	**0.36**	**0.53**	**2**
Season + Weekend + Sex	4	-3747.37	2.9	0.09	0.17	5	4	-3671.94	8.3	0.01	0.09	9	4	-2947.56	20.5	0.00	0.20	7
Season + Weekend + Reproductive status	4	-3747.36	2.9	0.09	0.17	4	4	-3671.91	8.3	0.01	0.09	8	4	-2947.25	19.9	0.00	0.22	6
Season + Weekend + Age	4	-3747.96	4.1	0.05	0.15	6	4	-3670.45	5.4	0.03	0.13	5	4	-2945.61	16.6	0.00	0.27	3

[a] K = number of parameters estimated in the model
[b] LL = log likelihood of the model
[c] w = AICc weight
[d] % D = percentage deviance explained by the model
[e] R = model ranking based on ΔAICc

Table 4. Parameter estimates for the top models (ΔAICc < 2) explaining bear distance to Cadomin, distance to road, and distance to trail.

Model rank	Variable	Category	Distance to Cadomin				Distance to road				Distance to trail			
			β[a]	Robust SE	95% CI		β[a]	Robust SE	95% CI		β[a]	Robust SE	95% CI	
1	Individual[b]	G023					-4.000	24.556	-52.129	44.128	18.275	10.386	-2.082	38.631
		G055					-68.613	35.130	-137.466	0.240	16.525	18.805	-20.322	53.382
		G111					89.632	32.820	25.307	153.958	73.506	22.845	28.731	118.281
		G112					88.809	31.874	26.338	151.281	-20.525	10.549	-41.200	0.151
		G113					48.113	24.814	-0.522	96.748	3.743	10.040	-15.935	23.422
	Season[c]	Hypophagia	-70.800	13.336	-96.938	-44.663								
		Hyperphagia	-104.321	11.799	-127.446	-81.196								
2		G023									16.852	10.341	-3.416	37.120
		G055									21.321	19.548	-16.992	59.633
		G111									67.208	24.130	19.913	114.504
		G112									-13.713	11.009	-35.290	7.865
		G113									3.056	10.569	-17.658	23.770
	Season[c]	Hypophagia	-68.767	13.279	-94.793	-42.741					-13.719	8.355	-30.094	2.655
		Hyperphagia	-104.192	11.633	-126.994	-81.391					-3.706	7.588	-18.578	11.166
	Weekend[d]		-21.435	11.161	-43.310	0.439					-4.960	6.538	-17.774	7.854

[a] Parameter estimate
[b] Bear G040 was withheld as the base outcome because it is the individual that became a problem bear
[c] Mesophagia was withheld as the base outcome because it was hypothesized to have the greatest risk of human–bear encounter
[d] Workday was withheld as base outcome because weekend was hypothesized to have the greatest risk of human–bear encounter

et al. 1994).

Female G040 did not differ substantially in use of space from most other bears using areas near Cadomin, but having cubs might have decreased the human tolerance of her and her cubs. With the exception of G040, the other research bears and potentially other (unmonitored) individuals in the area, even though close and sometimes seen by residents, were not reported as problems; only 3 of 14 reports recorded during 11 years revealed clear negative demeanors. Sighting a bear or other large carnivore will trigger differing human attitudes (Kellert et al. 1996) and varying responses. Each person's tolerance or acceptance, knowledge, experience, and fear ultimately dictate whether the sighting is reported, thus possibly determining the fate of the animal. Under rigorous scrutiny, information from public sightings can be used proactively to prevent conflicts, as long as a common framework is used for distinguishing between bear sightings and bear conflicts (Hopkins III et al. 2010).

We have shown that seasonality and individual variability influence patterns of bear space use but found that whether a bear becomes a problem is not easy to predict a priori. Stochastic factors as well as human dimensions likely play a substantial role in a bear's susceptibility to seeking food in human settlements. Additional variables that likely influence space use behavior are learning, memory, hunger motivation, chance encounters of rich food sources such as ungulate carcasses, or interactions with other grizzly bears, black bears, or wolves.

During the 8-year study period, Cadomin and the area within 500 m of the settlement were largely avoided by bears, as shown by the sparsity of our GPS radio collar data. None of the 9 adult bears we monitored had >4% of GPS locations within 500 m of town (Appendix 2). Although human distances beyond 100 m from bear attractants have been suggested as relatively safe (Creachbaum et al. 1998), our data showed that all bears had locations within 100 m from Cadomin. When all data within 500 m of Cadomin were considered, we showed that a minimum of 10 adult grizzly bears used this area during the study period to perform varied behaviors, including ungulate consumption, which is known to trigger aggressive behavior in some bears as a carcass defense mechanism (Herrero and Higgins 2003). The lack of consistent patterns of bear activity within specific seasons or by weekday, as well as absence of a seasonal pattern for reported conflict occurrence, makes it difficult to formulate management suggestions for specific times of the year or in relation to weekend human activity. Preventative measures that minimize the chance of encounters are the most effective solution to alleviate conflict between humans and grizzly bears as well as large carnivores in general (Löe and Röskaft 2004). Public education programs could focus on bear behavior; bear attractant management; and safe living, recreating, or working within bear range. Three essential precautions are (1) storing attractants away from where bears can access them (e.g., by using electric fencing, or bear-proof bins), (2) travelling in groups outside settlements, while being aware of surroundings, and (3) carrying non-lethal deterrents within reach (Herrero 2002, Quigley and Herrero 2005). With expanding human settlements and access in grizzly bear range, we expect increasing numbers of human–bear encounters, which underline the need to continue the implementation of initiatives such as Alberta Government's BearSmart program (AESRD 2012).

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Appendix 1. Mean bear distances to settlement, roads, and trails based on GPS radio collar data recorded within 500 m of Cadomin, Alberta, Canada during 2000–2010.

	Bear ID	Distance to Cadomin			Distance to road			Distance to trail			# years of monitoring
		Hypophagia	Mesophagia	Hyperphagia	Hypophagia	Mesophagia	Hyperphagia	Hypophagia	Mesophagia	Hyperphagia	
Research	G023	331	420	266	241	383	233	68	80	80	6 (6)[c]
	G029[a]	480			481			60			4 (1)[c]
	G037[a]			277			309			60	3 (1)[c]
	G040[b]			387			315			58	3 (2)[c]
	G055	387	245	122	134	263	140	152	64	41	1 (1)[c]
	G111	218	385		241	356		87	147		3 (3)[c]
	G112	293			329			39			1 (1)[c]
	G113	313	382	270	306	300	253	50	68	69	2 (2)[c]
	G115[a]		408			400		30			2 (1)[c]
Problem	G040[b]	245	319		177	265		55	66		1 (1)[c]
	378615[a]	314			335			34			N/A
	380139[a]			85			30			0	N/A
	All bears[d]	323 (298)	360 (350)	235 (261)	281 (238)	328 (313)	213 (235)	64 (75)	85 (85)	51 (62)	26 (19)[c]

[a] Locations excluded from analyses because of small sample size
[b] Research bear wearing collar becoming problem animal in mesophagia. Bear was subsequently captured and relocated by Alberta ESRD
[c] Number of monitoring years. In brackets, number of years with occurrence within 500 m of Cadomin
[d] Bear distances based on GPS locations within 500 m of Cadomin. In brackets, bear distances for the 6 bears used in statistical analyses

Appendix 2. Grizzly bear GPS location data recorded along 8 years of monitoring during 2000–2010.

Bear status	Bear ID	Sex	Total # GPS locations (T)	# GPS locations within 500 m of Cadomin (C)	Proportion of GPS locations near Cadomin (C/T)	# years of monitoring
Research	G023	Female	7,623	227	0.03	6 (6)[c]
	G029[a]	Male	2,461	1	0.00	4 (1)[c]
	G037[a]	Female	2,817	1	0.00	3 (1)[c]
	G040[b]	Female	1,527	10	0.01	3 (2)[c]
	G055	Male	443	15	0.03	1 (1)[c]
	G111	Female	6,061	31	0.01	3 (3)[c]
	G112	Male	1,317	23	0.02	1 (1)[c]
	G113	Female	5,684	216	0.04	2 (2)[c]
	G115[a]	Male	4,600	1	0.00	2 (1)[c]
Problem	G040[b]	Female	1,919	37	0.02	1 (1)[c]
	378615[a]	Male	140	2	0.01	N/A
	380139[a,d]	Male	3	1	0.33	N/A
All bears	All bears[e]	Male & Female	34,595 (N/A)	565 (559)	N/A	26 (19)[c]

[a] Locations excluded from analyses because of small sample size
[b] Research bear wearing collar becoming problem animal in mesophagia. Bear was subsequently captured and relocated by Alberta ESRD
[c] Number of monitoring years. In brackets, number of years with occurrence within 500 m of Cadomin
[d] Occurrence record based on observing Band/Collar/Tag (Alberta ESRD survey type category denoting that the bear was not wearing a GPS radio collar)
[e] Total number of GPS locations within 500 m of Cadomin. In brackets, number of locations used in statistical analyses

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