Home Range, Movements, and Denning Chronology of the Grizzly Bear (*Ursus arctos*) in West-Central Alberta

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An understanding of the natural history of the Grizzly Bear (*Ursus arctos*) is important for recovery planning. We present data on home range size, movements and denning chronology collected using Global Positioning System (GPS) collars on Grizzly Bears in west-central Alberta. Mean annual kernel estimates for adult (1034 ± 656 (SD) km^2) and subadult (1298 ± 1207 km^2) males were larger than those for females with cubs of the year (213 ± 212 km^2) and lone adult females (337 ± 176 km^2) but not different from sub-adult females, females with yearlings, or females with $\geq$ 2-yr old cubs ($P > 0.05$). Mean rates of movement among female age–reproductive classes were different from each other ($Z_9 < 2.70$, $P > 0.05$) but not different from sub-adult males ($Z_9 < 2.70$, $P > 0.05$). Rates of movement of adult males were significantly different only from those of females with cubs of the year ($Z_9 = 3.94$, $P = 0.001$). The greatest amount of movement occurred in June and the least in October. Bears traveled fastest in the morning and evening and slowest at night. Pregnant females had the longest denning period (175 days, $\pm$ 16 days SD). No difference was detected in denning duration among the remaining five age–sex–reproductive classes ($P > 0.05$). GPS collars provided large location datasets from which accurate home range estimates, hourly movement rates, and precise denning dates were determined. Examining similarities and differences in the basic biology of Grizzly Bears from various locations will improve our understanding of the plasticity of this species and the potential impacts of habitat and climate change.

Key Words: Grizzly Bear; *Ursus arctos*; home range; movement; denning chronology; GPS collar; Alberta

Introduction

Many populations of the Grizzly Bear (*Ursus arctos*) are at some level of endangerment, and a better understanding of the species' basic biology is important to aid conservation efforts (Servheen 1993; Alberta Sustainable Resource Development 2008*). The collection and collation of biological data from across the range of the Grizzly Bear provides an opportunity to compare current data with those in past studies as well as studies from other areas, so that we might better understand the plasticity and adaptability of this species. Increased knowledge of its basic biology may also increase our ability to predict impacts of landscape change, habitat modification, and climate change on Grizzly Bear populations.

The purpose of this paper is to present information on Grizzly Bear home range size, movements, and denning chronology in west-central Alberta from bears equipped with Global Positioning System (GPS) collars in west-central Alberta. We compare age–sex classes in terms of home range size, movements, and denning chronology. Further, we compare movements during different months and different times of day.

Despite numerous studies of the Grizzly Bear in west-central Alberta addressing specific research topics using GPS collar data (e.g., Nielsen *et al.* 2002, 2003, 2004, 2006, 2010; Munro *et al.* 2006; Berland

et al. 2008; Roever *et al.* 2008, 2010; Graham *et al.* 2010; Cristescu *et al.* 2011; Northrup *et al.* 2012; Stewart *et al.* 2012), basic biological data on home range, movements and denning chronology have not yet been presented. Earlier studies using Very High Frequency (VHF) radio collars have provided estimates of home range size, movements, and denning chronology; however, improvements in the quality and quantity of location data made possible by GPS collar technology should increase our understanding of these characteristics. We compare our results with those from earlier studies in Alberta that relied on VHF technology, as well as studies throughout the circumpolar range of the Grizzly Bear.

Study Area

We focused on two genetically distinct Grizzly Bear populations in west-central Alberta (Proctor *et al.* 2012): the Yellowhead population unit (YPU; 53°14'53"N, 117°25'12"W) and the Grande Cache population unit (GCPU; 44°10'19"N, 77°13'44"W). The location of the YPU includes southern Jasper National Park in the Rocky Mountains (Figure 1). The GCPU is located directly north of the YPU and covers the northern part of Jasper National Park and the Wilmore Wilderness area, both in the Rocky Mountains (Figure 1). Elevations are highest (up to 2700 m) in the western portion
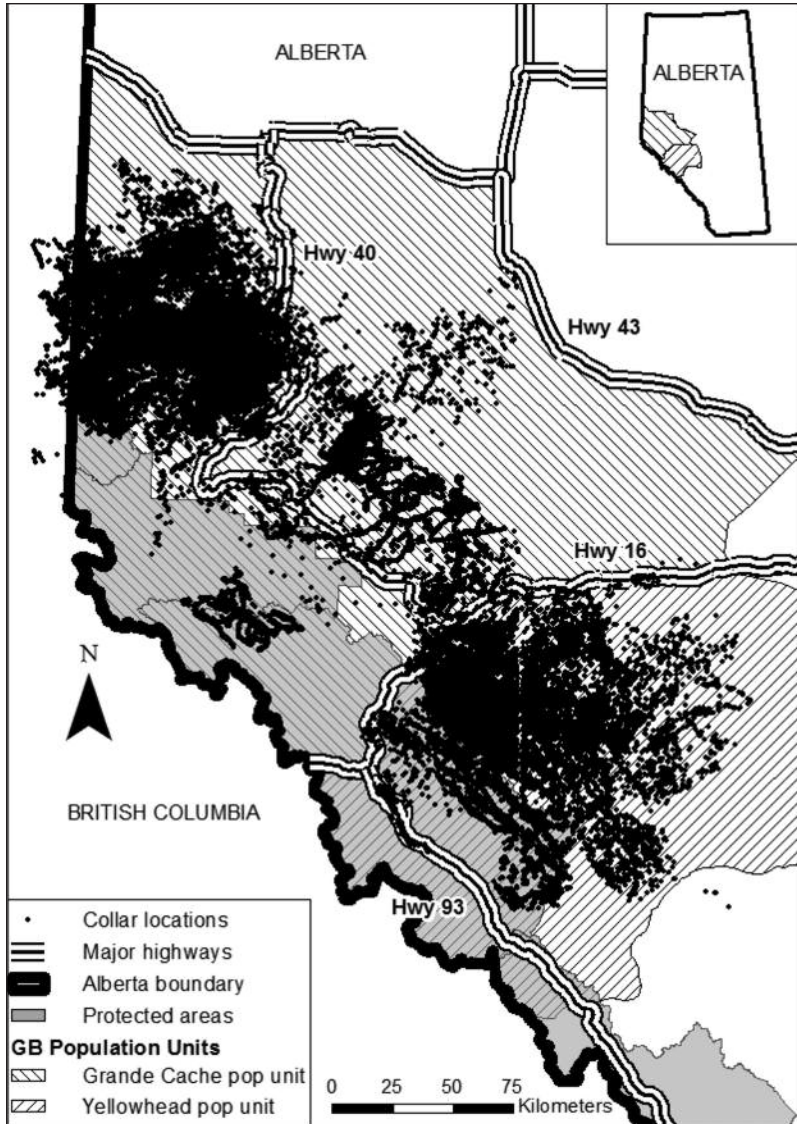
FIGURE 1. Location data for Grizzly Bears (*Ursus arctos*) collected using Global Positioning System collars from 1999 to 2010 for the Yellowhead and Grande Cache population units in west-central Alberta, Canada.

of both areas and decline eastward to approximately 900 m. This elevation gradient results in a diversity of ecosites (Beckingham *et al.* 1996*) including alpine/subalpine meadows; forests dominated by coniferous species consisting of Lodgepole Pine (*Pinus contorta*), White Spruce (*Picea glauca*), Black Spruce (*P. mariana*), or Englemann Spruce (*P. englemannii*); mixed forests comprising conifers with Trembling Aspen (*Populus tremuloides*) or Balsam Poplar (*P. balsamifera*); and wet meadow complexes. Both locations include large cleared areas, seismic lines, pipelines, and roads associated with timber harvesting, oil and gas exploration and development, and open-pit coal min-

ing. A number of recreational activities also occur within these areas, including hunting, trapping, use of all-terrain vehicles, camping, hiking, and mountain biking. A regulated spring hunt for American Black Bears (*Ursus americanus*) occurred during the study. A limited-entry hunt for Grizzly Bears occurred during spring 1999–2005, but ceased in 2006.

Methods
Captures
Grizzly Bears in the YPU and GCPU were captured and radio-collared from 1999 to 2010 and 2003 to 2010, respectively. Capture methods included the use of cul-

vert traps, leg-hold snares, and aerial darting from a helicopter. In 2010, we terminated the use of snares because of potential long-term capture impacts (Cattet *et al.* 2003, 2008). From 2010, capture techniques involved aerial darting and culvert traps with satellite alarm systems, designed to minimize the amount of time bears were confined in the trap. Aerial darting via helicopter occurred in open areas, such as alpine/subalpine meadows and logged areas. Most snares and culvert traps were placed in forested areas where aerial darting was not feasible. Sites were usually < 100 m from a road or other access feature type; however, some sites were accessible only by helicopter. Capture protocols were approved by the Canadian Council on Animal Care for the safe handling of bears and approved annually by the University of Saskatchewan and the Government of Alberta animal care committees.

Grizzly Bears were fitted with a GPS radio collars, including Simplex, Tellus, or Tellus Satellite collars (Televilt [now Followit], Lindesberg, Sweden); or Advanced Telemetry Systems (ATS; Isanti, Minnesota, USA) collars. All collars emitted a unique VHF radio signal to locate the bear. From 1999 to 2005, Simplex collars were used and typically programmed to obtain a location every 4 h during the non-denning period. Collars deployed in the spring were retrieved in the fall of the following year (1.5 years later) using a remote drop-off mechanism, which allowed retrieval without the need for recapture. Improvements in Tellus collars and battery life occurred in 2004. The new collars were able to provide hourly locations during the non-denning period over 1.5 years. Remote data downloads were possible for all versions of Televilt collars, allowing data to be obtained even if the collar was not retrieved at the end of its life. In 2010, one bear was collared with a Tellus Satellite GPS collar, and data from this collar were remotely obtained from a service provider. ATS collars were used from 1999 to 2008. As they did not have the remote data retrieval option, collars were retrieved using a remote drop-off mechanism at the end of the battery life, typically 8 months. Grizzly Bears were also fitted with a VHF ear tag transmitter (ATS), so that they could be located for collar removal in case the collar failed.

A premolar tooth was extracted from captured bears and sent to a commercial laboratory for age determination based on cementum annuli counts (Matson *et al.* 1993*). Age classes used in our analysis included adult (≥ 5 years) and independent sub-adult (2 to < 5 years). Bears younger than 2 years were not collared, but were given an ear tag transmitter, for possible relocation and capture in successive years. We recorded whether captured females were accompanied by cubs of the year (COY), yearlings, or older cubs (≥ 2 years old).

Home range

We calculated annual 100% minimum convex polygons (MCP) and 95% kernel home ranges using the program ABODE (Laver 2005*) in a Geographic Information System (GIS). We determined both MCPs and 95% kernels (Worton 1987) to allow comparisons with other studies. Fixed biweight kernels (Sliverman 1986) were calculated using a volume contouring method. We used a least-squares smoothing factor (Seaman and Powell 1996) and a grid cell size of 300 m^2. Kernels were standardized using the unit variance method (Silverman 1986).

We included a home range estimate only if data locations were available from May to October to ensure that the entire year was represented (Arthur and Schwartz 1999; Belant and Follmann 2002; Girard *et al.* 2002). In addition, each home range estimate required a minimum of 100 days of location data or it was excluded from the analysis (Arthur and Schwartz 1999; Belant and Follmann 2002). If a bear generated more than one year of location data for the same age or reproductive class, only the data for the year with the greatest number of locations were used. We determined mean 100% MCP and 95% kernel home range estimates for seven age–sex–reproductive classes: female with COY, female with yearlings, females with ≥ 2 year olds, lone adult females, sub-adult females, sub-adult males, and adult males (Table 1). Only the 95% kernel estimates were statistically compared among the seven age–sex–reproductive classes.

Movement rates

We used Visual Basic in Access Microsoft (version 2003) to determine the distance between successive

TABLE 1. Home range estimates, calculated as mean 100% minimum convex polygons (MCP) and 95% kernels, for Grizzly Bears (*Ursus arctos*) in west-central Alberta, by age–sex–reproductive class based on Global Positioning System collar data. Kernel estimates for classes with different numbered superscripts are statistically different ($P < 0.05$) based on non-parametric multiple comparison tests.

Age–sex–reproductive class	n	Mean annual 100% MCP (SD, range), km^2	Mean annual 95% kernel (SD, range), km^2
Female with COY	11	370 (250, 119–1025)	213 (212, 62–808)[1]
Female with yearling	9	735 (822, 267–2904)	472 (527, 136–1848)[1,2]
Female with ≥ 2 year old	7	722 (464, 202–1554)	494 (428, 105–1397)[1,2]
Sub-adult female	14	732 (376, 222–1447)	394 (231, 86–836)[1,2]
Lone adult female	22	615 (311, 200–1260)	337 (176, 107–706)[1]
Sub-adult male	10	2152 (1469, 509–4993)	1298 (1207, 354–4282)[2]
Adult male	14	1824 (1006, 336–3154)	1034 (656, 203–2071)[2]

locations and calculate hourly movement rates. We chose 1-h time units because these were our most fine-scaled temporal data and hourly readings were possible after 2004 using improved collars that allowed a collar to last 1.5 years at an hourly fix rate during the non-denning period. We only measured movements outside the denning period because previous research has shown that Grizzly Bear movements are reduced before den entry (Nelson *et al.* 1983; Friebe *et al.* 2001; Manchi and Swenson 2005) and immediately after den exit (Craighead and Craighead 1972; Nelson *et al.* 1983; Schwartz *et al.* 2010). To exclude the denning period, we removed data locations within 500 m of known den sites and within an average of 7 days of den entry and exit dates (see below). Also, the movement of many Grizzly Bears is reduced for up to a month after a capture event (Cattet *et al*. 2008); thus, location data collected within 30 days of a capture were also removed from analysis. For movement rates, we pooled females with yearlings and older cubs into one class (females with yearlings+) to increase sample size and produce six age–sex–reproductive classes.

Denning chronology

We determined den entry and exit dates and time in the den from collar data. Collars were programed to acquire at least one location every day during the denning period because the manufacturer recommended keeping the batteries active rather than shutting them off completely for months at a time. Typically, when bears entered their dens, GPS collars were unable to acquire a location even though an attempt was made; therefore, the day the collar consistently stopped recording locations was considered to be the day the bear entered the den. Den exit dates were determined in a similar fashion, as the day the collar began to signal locations consistently again in the spring. Time in the den was calculated based on data from bears with known entry and exits dates for the same denning period.

Statistical analysis

We tested for normality and homoscedasticity using a Shapiro-Wilk test for normality and a Bartlet's test for equal variances as well as visual examination of standardized normal probability plots. When data were not normal, appropriate transformations were applied or nonparametric analyses were used. We used a Krusal-Wallis test to determine whether mean kernel sizes differed among age–sex–reproductive classes and subsequent nonparametric multiple comparison tests to determine which means were significantly different from others (Zar 1984). We graphed the hourly movement rates for each age–sex–reproductive class by hour of the day and month of the year. We used a mixed effects multiple linear regression on log transformed hourly movement rates with bears as the random effects factor to determine whether movement rates differed across the fixed effect factors of age–sex–reproductive class, activity period, and month. We then conducted

multiple comparisons of the marginal means for the fixed effect factors using a Bonferroni adjustment to determine where differences occurred. We used ANOVA to compare den duration across age–sex–reproductive class followed by a Tukey post-hoc multiple comparison to determine which classes were different from others. Statistical analyses were conducted using Stata SE (v. 12.0 for Windows; StataCorp LP, College Station, Texas). We used an alpha level of 0.05.

Between 1999 and 2010, we captured 40 females and 31 males from the YPU and 18 females and 36 males from the GCPU. A total of 251 capture events took place. Individual bears were captured on average 2.5 ± 1.8 times in the YPU and 1.4 ± 0.8 times in the GCPU. A total of 53 Grizzly Bears from the YPU and 46 from the GCPU were collared. Collars functioned on bears from the YPU for an average of 476 ± 445 days, range = 13–2025 days) and 346 days on bears from the GCPU (SD 396 days, range 3–2072 days). In total 659 744 GPS locations were collected during this period.

Home range size

We estimated 97 annual 100% MCP and 95% kernel home range sizes for 59 Grizzly Bears, using location data collected from 1999 to 2010. We included 21 bears more than once because their age or reproductive class changed over time. A mean of 1691 locations (SD 1962, range 203–9804) were used in the MCP and kernel estimates. The mean kernel size across the seven age–sex–reproductive classes differed significantly ($H_6 = 32.31$, $P < 0.001$; Table 1). Kernel sizes of adult and sub-adult males were not significantly different from each other ($P > 0.05$, Table 1) or from those of sub-adult females ($P > 0.05$), females with yearlings ($P > 0.05$) or females with $\geq$ 2-year-old cubs ($P > 0.05$), but they were significantly larger than females with COY (adult males: $Q_7 = 4.56$, $P < 0.05$; sub-adult males: $Q_7 = 4.82$, $P < 0.05$) and lone adult females (adult males: $Q_7 = 3.33$, $P < 0.05$; sub-adult males: $Q_7 = 3.64$, $P < 0.05$). There were no differences in home range size among the five female age–reproductive classes ($P > 0.05$, Table 1).

Movements

Hourly location data from 39 Grizzly Bears in the YPU and GCPU provided 87 959 hourly movement rates. Except for females with COY, mean movement rates for all other age–sex–reproductive classes tended to be greatest in June; the greatest movement rates for females with COY occurred in August (Figure 2). Movement rates generally declined after June, although adult males showed an increase in September and October (Figure 2). Movement rates by hour of the day showed a bimodal pattern, with four distinct activity periods (Figure 3). Bears travel slowly at night (2200–0500), quicker during the morning (0600–1100) and evening (1700–2100), and moderately in the afternoon (1200–1600). These four activity periods were used in the regression analysis.
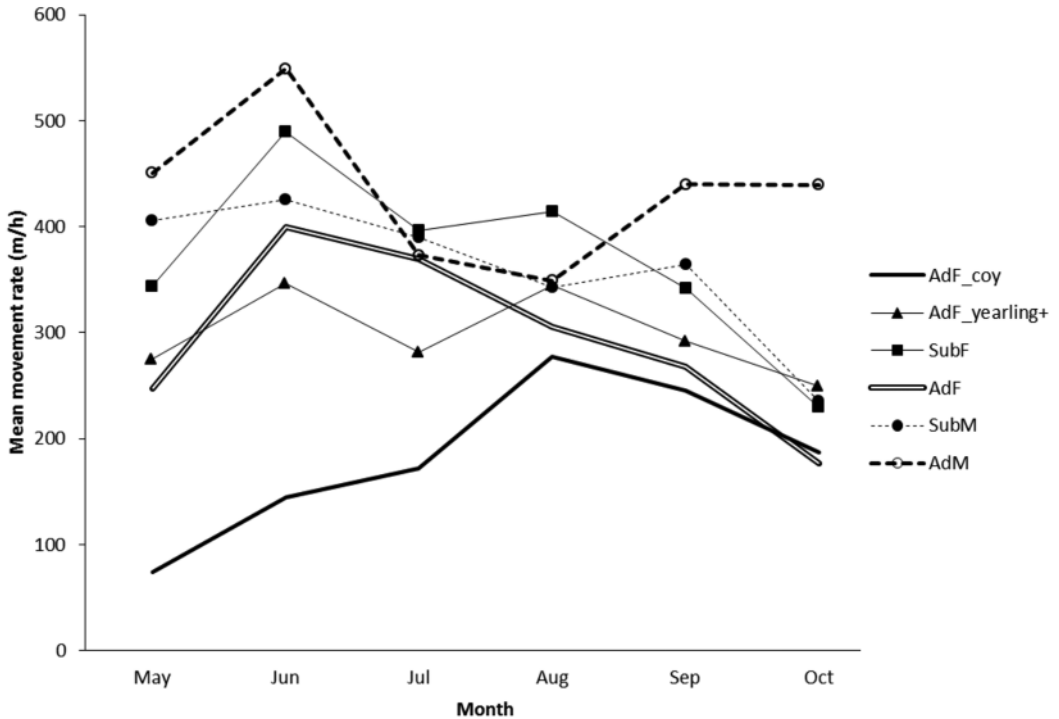
FIGURE 2. Mean rates of movement by month for six age–sex–reproductive classes of Grizzly Bears (*Ursus arctos*) in west-central Alberta. AdF_coy = females with cub of the year, AdF_yearling+ = females with yearling or older cub, SubF = sub-adult females, AdF = lone adult females, SubM = sub-adult males, AdM = adult males.

TABLE 2. Results for the fixed effect factors (age–sex–reproductive class, month and activity period) used in the multiple linear regression analysis to explain hourly movement rates (grouped by bear). Lone adult females, the month of May and the morning activity period were reference categories. Data were log transformed to accentuate heteroscedasticity.

Factor	Age–sex–reproductive class	Coefficient	Standard deviation	Z	$P > |z|$	95% confidence interval	
Class	Female with coy	−0.0742	0.0128	−5.79	0.000	−0.0993	−0.04905
	Female with yearling+	0.0419	0.0105	3.96	0.000	0.0211	0.0626
	Sub-adult female	0.1293	0.0098	13.22	0.000	0.1101	0.1485
	Sub-adult male	0.0157	0.0415	0.38	0.704	−0.0655	0.0970
	Adult male	0.0839	0.0390	2.15	0.032	0.0074	0.1604
Month	June	0.1291	0.0099	13.03	0.000	0.1097	0.1486
	July	0.1858	0.0091	20.46	0.000	0.1680	0.2036
	August	0.1578	0.0091	17.28	0.000	0.1399	0.1756
	September	0.0680	0.0093	7.29	0.000	0.0497	0.0863
	October	−0.1326	0.0091	−14.55	0.000	−0.1505	−0.1147
Activity period	Afternoon	−0.1606	0.0068	−23.55	0.000	−0.1740	−0.1473
	Evening	0.0828	0.0068	12.17	0.000	0.0694	0.0961
	Night	−0.5367	0.0062	−86.19	0.000	−0.5489	−0.5245
Intercept		2.0634	0.0261	79.09	0.000	2.0122	2.114

Age–sex–reproductive class (six classes), activity period (morning, afternoon, evening, and night) and month (May to October) were significant predictors of hourly movement rates (Tables 2 and 3). Comparison of marginal means indicated that all 6 months were significantly different from each other ($Z_9 < 40.57, P \leq 0.01$ for all 15 comparisons; Table 4). The fastest mean movement rate occurred in June and the slowest in October. Likewise, all four activity periods were significantly different from each other ($Z_2 < 94.88, P < 0.01$ for all six comparisons; Table 5). Bears moved fastest in the evening followed by the morning and afternoon, with the slowest mean movement rate occurring at night.
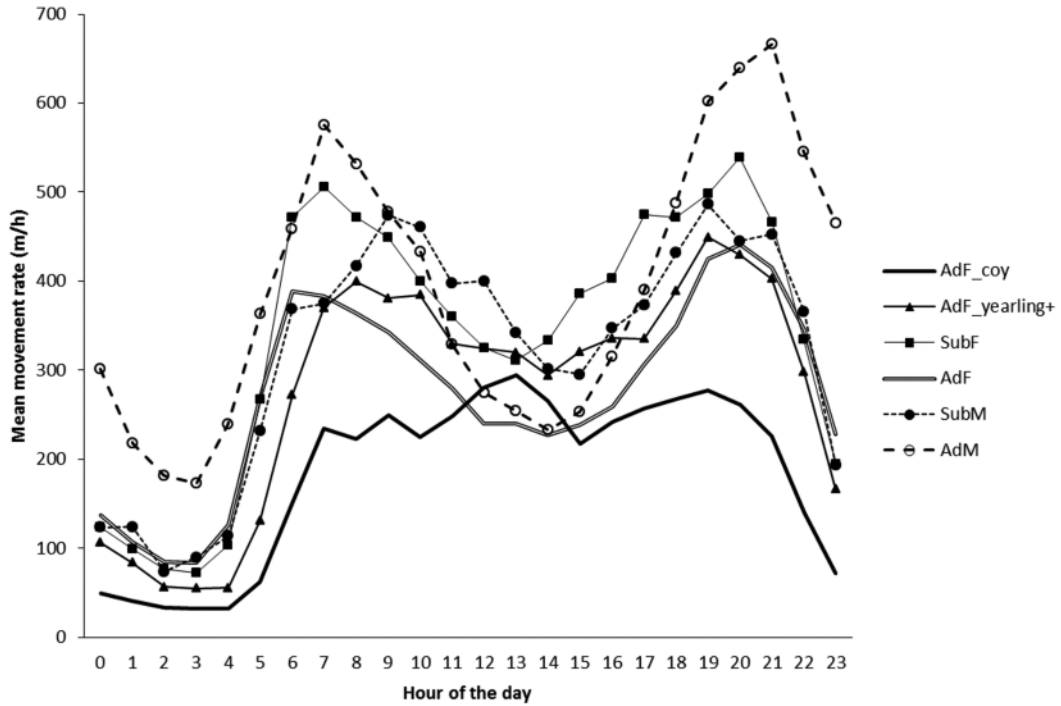
FIGURE 3. Mean rates of movement by hour of the day for six age–sex–reproductive classes of Grizzly Bears (*Ursus arctos*) in west-central Alberta. AdF_coy = females with cub of the year, AdF_yearling+ = females with yearling or older cub, SubF = sub-adult females, AdF = lone adult females, SubM = sub-adult males, AdM = adult males.

TABLE 3. Results for bear as the random effect factors used in the multiple linear regression analysis to explain hourly movement rates. Data were log transformed to accentuate heteroscedasticity.

Random effects for bear	Estimate	Standard deviation	95% confidence interval
Standard deviation of intercept	0.1117	0.0139	0.0874–0.1426
Standard deviation of residuals	0.6903	0.0016	0.6871–0.6935

TABLE 4. Mean hourly movement rates of Grizzly Bears (*Ursus arctos*) in west-central Alberta by month. Post-hoc comparisons with Bonferroni adjusted P values are provided.

Month	n	Mean movement rate, m/h (SD)*	June	July	August	September	October
May	10 657	287 (487.7)	$Z_9 = 13.03$ $P < 0.001$	$Z_9 = 20.46$ $P < 0.001$	$Z_9 = 17.28$ $P < 0.001$	$Z_9 = 7.29$ $P < 0.001$	$Z_9 = -14.55$ $P < 0.001$
June	10 298	391 (602.3)		$Z_9 = 6.39$ $P < 0.001$	$Z_9 = 3.19$ $P = 0.001$	$Z_9 = -6.63$ $P < 0.001$	$Z_9 = -28.38$ $P < 0.001$
July	17 429	346 (473.5)			$Z_9 = -3.78$ $P < 0.001$	$Z_9 = -15.14$ $P < 0.001$	$Z_9 = -40.57$ $P < 0.001$
August	18 132	343 (478.9)				$Z_9 = -11.76$ $P < 0.001$	$Z_9 = -37.54$ $P < 0.001$
September	15 461	320 (497.7)					$Z_9 = -25.05$ $P < 0.001$
October	15 982	251 (497.8)					

*SD = standard deviation.

TABLE 5. Mean hourly movement rates of Grizzly Bears (*Ursus arctos*) in west-central Alberta by activity period. Post-hoc comparisons with Bonferroni adjusted *P* values are provided.

Activity period	n	Mean movement rate, m/h (SD)*	Afternoon	Evening	Night
Morning	22 526	403 (541.8)	$Z_2 = -23.55$ $P < 0.001$	$Z_2 = 12.17$ $P < 0.001$	$Z_2 = -86.19$ $P < 0.001$
Afternoon	18 863	296 (447.3)		$Z_2 = 34.28$ $P < 0.001$	$Z_2 = -57.29$ $P < 0.001$
Evening	19 032	448 (563.7)			$Z_2 = -94.88$ $P < 0.001$
Night	27 538	185 (420.7)			

*SD = standard deviation.

TABLE 6. Mean hourly movement rates of Grizzly Bears (*Ursus arctos*) in west-central Alberta, by age–sex–reproductive class. Post-hoc comparisons with Bonferroni adjusted *P* values are provided. Non-significant (*P* > 0.05) differences are in bold.

| Age–sex–reproductive class	n	Mean movement rate, m/h (SD)*	Female with yearling+	Sub-adult female	Lone adult female	Sub-adult male	Adult male
Female with COY	7 354	191 (317.8)	$Z_9 = 9.28$ $P < 0.001$	$Z_9 = 12.69$ $P < 0.001$	$Z_9 = -5.79$ $P < 0.001$	**$Z_9 = 2.12$** **$P = 0.515$**	$Z_9 = 3.94$ $P = 0.001$
Female with yearling+	14 645	297 (449.6)		$Z_9 = 6.12$ $P < 0.001$	$Z_9 = 3.96$ $P = 0.001$	**$Z_9 = -0.62$** **$P = 1.000$**	**$Z_9 = 1.06$** **$P = 1.000$**
Sub-adult female	15 048	366 (506.4)			$Z_9 = 13.22$ $P < 0.001$	**$Z_9 = -2.70$** **$P = 0.102$**	**$Z_9 = -1.14$** **$P = 1.000$**
Lone adult female	28 160	292 (459.6)				**$Z_9 = 0.38$** **$P = 1.00$**	**$Z_9 = 2.15$** **$P = 0.47$**
Sub-adult male	7 584	342 (522.3)					**$Z_9 = -2.63$** **$P = 0.128$**
Adult male	15 168	408 (649.7)					

*SD = standard deviation.
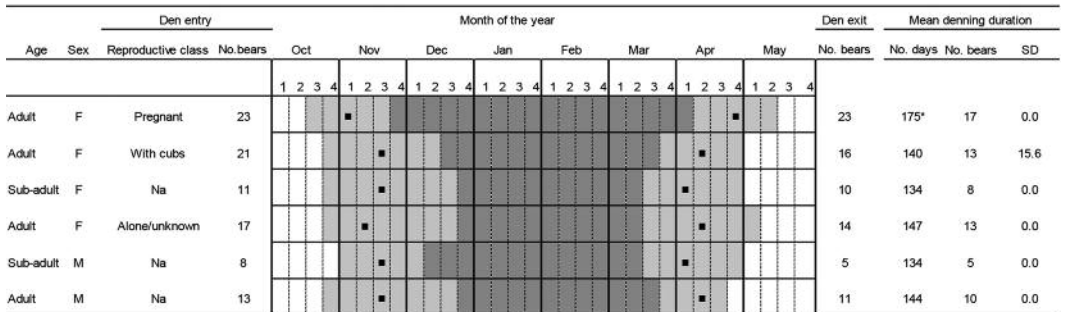
FIGURE 4. Den entry and exit dates by quarter month and age–sex–reproductive class for Grizzly Bears (*Ursus arctos*) in west-central Alberta, determined from Global Positioning System collar data from 1999 to 2010. Small black squares indicate mean den entry or exit dates, light shading indicates the range of entry and exit dates and dark shading indicates when all bears were in their dens. Den time was longer for pregnant females than for the other five classes (Tukey post-hoc multiple comparison test; *P* < 0.002) and is indicated by an asterisk. Females with cubs represent females accompanied with any aged cub at den entry.

Adult males and sub-adult females had the fastest mean movement rates (408 m/h and 366 m/h, respectively) but adult and sub-adult males had the largest standard deviations (650 and 522, respectively; Table 6). Comparisons of marginal means (Table 6) showed that adult males were significantly faster than females with COY ($Z_9 = 3.94$, $P = 0.001$) but not different from the remaining age–sex–reproductive classes ($Z_9 < 2.63$, $P > 0.05$) while sub-adult males were not different from any of the age–sex–reproductive classes ($Z_9 < 2.70$, $P > 0.05$). Females with COY had the slowest movement rate, followed by lone adult females, females with yearlings, and older and sub-adult females; all which were significantly different from each other ($Z_9 > 3.94$, $P < 0.01$).

Denning

Different age–sex classes exhibited different denning chronology (Figure 4). Pregnant females entered dens first, in early November, followed by lone adult females, females with cubs of all ages and adult males in close succession. Sub-adult males and females entered their dens last, in late November (Figure 3). Conversely, Grizzly Bears exited their dens in the reverse order with sub-adult males and females emerging first, in early April, followed by adult males, females with yearlings or older, lone adult females, and finally, females with COY, in late April. Denning duration varied among age–sex–reproductive class ($F_{5,60}$ = 8.78; $P < 0.001$). Pregnant females had the longest denning duration, significantly longer than lone adult females ($q_{60,6}$ = −4.04, $P = 0.002$), females with yearlings and older ($q_{60,6}$ = −4.99, $P < 0.001$), adult males ($q_{60,6}$ = −4.17; $P = 0.001$), sub-adult females ($q_{60,6}$ = −5.04, $P < 0.001$), and sub-adult males ($q_{60,6}$ = −4.27; $P = 0.001$). There were no significant differences in length of denning duration among the other age–sex–reproductive classes ($P > 0.05$). Pregnant females spent the longest time in dens, (approximately 48% of the year), whereas sub-adults of both sexes spent the least amount of time in dens, approximately 38% of the year) (Figure 3).

Discussion

The age and sex of a Grizzly Bear are important factors influencing home range size and rates of movement throughout their circumpolar range (Pearson 1975*; Blanchard and Knight 1991; Mace and Waller 1997; McLoughlin *et al.* 1999; Dahle and Swenson 2003a; Stevens and Gibeau 2005; Ciarniello *et al.* 2009; Edwards *et al.* 2009). Adult males typically have large home ranges and move quickly, probably, in part, because they are searching for reproductive females (Blanchard and Knight 1991; Dahle and Swenson 2003a; Krofel *et al.* 2010). Our results support this searching behaviour: the fastest movements by adult males occurred in June, which corresponds to the peak mating period in our area (Stenhouse *et al.* 2005). Large ranges of movement by adult males have also been explained by individuals travelling more in search of food to support a large body mass (McNab 1963; McLoughlin *et al.* 1999) and this could also be the reason for the increase in movement rates observed among adult males in the fall during our study. Fall is the period of hyperphagia (Nielsen *et al.* 2004); thus, adult males may travel more at this time in search of food to fatten up before denning. Adult males may also be actively gathering information on other bears within their home range for the following year (Dahle and Swenson 2003a). The relatively fast movements of females with yearlings and older cubs compared with those of lone adult females may also be a result of searching for food to satisfy the energy demands of the female and her growing cubs (Blanchard and Knight 1991).

The slow movements of females with COY have been attributed to the reduced mobility of the COY and an avoidance of males to reduce possible infanticide (Blanchard and Knight 1991; Dahle and Swenson 2003a,b; Steyaert 2012). However, home range size of females with COY was not significantly different from that of other female age–reproductive classes. This is in contrast to findings for Grizzly Bears in Sweden (Dahle and Swenson 2003a), but similar to those in the Northwest Territories (McLoughlin *et al.* 1999). Dahle and Swenson (2003b) found that spring ranges of females with COY in Sweden were small, but expanded once the breeding season was over. Although we did not examine seasonal ranges, our mean monthly movement rates suggested that movements increased each month until August when rates were similar to those of lone adult females. We cannot say whether movement rates in May were slow because of limited COY mobility or to avoid infanticidal males, but home ranges of females with COY likely expand throughout the summer until they are similar in size to those of other female age–reproductive classes.

Our home range estimates for male and female sub-adults were based on whether the bear was independent and < 5 years of age. Because we did not distinguish between dispersing and philopatric individuals, our estimates likely included dispersing bears and, therefore, did not conform to the traditional definition of a home range (Burt 1943). Because sub-adult males disperse farther than sub-adult females (Blanchard and Knight 1991; Zedrosser *et al.* 2007), the likely inclusion of dispersing males resulted in a large home range estimate and standard deviation and could explain why our estimate was four times larger than the home range reported for philopatric sub-adult males in Sweden (Dahle *et al.* 2006).

The large variation in hourly movement rates by adult and sub-adult males and the conservative nature of the Bonferroni adjustment (Garcia 2004) could have resulted in missing significant differences (Type II error). The mean movement rate of sub-adult males was not different from the other age–sex–reproductive classes, and adult males' rate was only different from that of females with COY. Other researchers have documented differences in movement rates between the sexes (Blanchard and Knight 1991, McLoughlin *et al.* 1999). Perhaps of more interest is the large variability we found in male movement rates. Further work to look at movements by males and site visits to areas where different movement rates occurred are needed to understanding the observed differences.

The bimodal activity pattern displayed by Grizzly Bears in our study was similar to that reported for British Columbia (McCann 1991), Montana (Aune and Kasworm 1989*), and Europe (Roth 1983; Roth and

Huber 1986; Moe *et al.* 2007), but the mid-day inactive period was longer and appeared to be the main rest period for the European bears. In contrast, male Grizzly Bears in Wyoming were active throughout the night and rested in mid-afternoon while females showed a pattern similar to our adult females (Holm *et al.* 1999). Movement can be influenced by many factors including season, cover, temperature, food availability, age, sex, bear density, and human activities (Aune and Kasworm 1989*; McCann 1991; Dahle *et al.* 2006). In the future, the ability to compare movements with data of similar quality and quantity within a population over time and across populations may help us to better understand factors that influence movement rates.

Three studies conducted more than a decade ago within our study area also reported home range estimates (Pearson and Nolan 1976*; Russell *et al.* 1978*, 1979*; Horejsi and Stegenga 1981*; Horejsi and Slatter 1982*; Horejsi and Raine 1983*; Nagy *et al.* 1989*; Nagy and Haroldson 1990). These studies, which relied on VHF collars to obtain a location on a weekly or bi-weekly schedule, provided the foundation of our understanding of Grizzly Bear biology in Alberta. VHF-based home range estimates were typically based on < 50 locations and bear locations were likely missed when the animal had moved outside the survey area (Russell *et al.* 1979,* Dahle and Swenson 2003a, Collin *et al.* 2005); therefore, these studies likely underestimated the true home range size (Arthur and Schwartz 1999; Girard *et al.* 2002). However, similar to our results, their data showed that male bears were fast moving, MCPs for males were larger than those for females, and females with COY had the smallest MCPs.

Denning is believed to have evolved as a mechanism to endure periods with little food (Manchi and Swenson 2005); however, the triggers that cause a Grizzly Bear to enter and leave a den are not fully understood (Friebe *et al.* 2001). On a large scale, latitude explains some of the variability in denning period across the Grizzly Bear's range (Manchi and Swenson 2005): in Sweden (Manchi and Swenson 2005) and the Canadian north (McLoughlin *et al.* 2002) Grizzly Bears denned 10–30 days longer than in west-central Alberta, whereas, in Yellowstone, den time was 10–30 days shorter (Judd *et al.* 1986). However, latitude alone cannot explain all the differences in denning period as some Grizzly Bears on Kodiak Island, Alaska, do not den at all (Van Daele *et al.* 1989), and Grizzly Bears in British Columbia, at a latitude similar to that of our study area, denned more than 50 days longer (Ciarniello *et al.* 2005). Heavy snowfall (Craighead and Craighead 1972; Servheen and Klaver 1983; Friebe *et al.* 2001; Manchi and Swenson 2005) has been associated with den entry for some populations, while declines in food supply may have influenced den entry in others (Clevenger *et al.* 1990; Ciarniello *et al.* 2009). Precise denning dates, along with local weather and snow conditions, body

condition, and food supply information, are needed to improve understanding of den ecology within and across populations (K. Pigeon, unpublished data).

Denning duration has been related to a bear's fat stores prior to denning, its surface–volume ratio, den type, and reproductive status (Craighead and Craighead 1972; Schwartz *et al.* 1987; Ciarniello *et al.* 2005; Friebe *et al.* 2001; Manchi and Swenson 2005). A long denning duration for pregnant females has been documented for Grizzly Bears throughout their circumpolar range (Craighead and Craighead 1972; Ballard *et al.* 1982; Ciarniello *et al.* 2005; Friebe *et al.* 2001; Manchi and Swenson 2005). Early den entry by pregnant females may have more to do with reproductive physiology than environmental factors (Hissa *et al.* 1994; Friebe *et al.* 2001), and late den exit by females with COY may be a result of waiting until travel conditions are suitable for very young bears (Craighead and Craighead 1972). Small, young male bears had a longer denning duration than old, large males in southern Sweden (Manchi and Swenson 2005), while sub-adult females had a shorter denning duration than adult females (Friebe *et al.* 2001). We did not find a difference in denning duration among our sub-adults and adults. However, the sample size for sub-adult males was small and post-hoc multiple comparisons can increase the chance of conducting a Type II error (Zar 1984). Therefore, it is possible that we failed to recognize a significant difference among some age–sex–reproductive classes. Further work to examine the denning biology of Grizzly Bears in Alberta is currently underway.

Denning dates from the VHF studies that overlapped our study area were available for Jasper National Park (Russell *et al.* 1979*) and the Wapiti River area (Horejsi and Raine 1983*). These dates were often inexact, and denning duration was difficult to determine when spring and fall monitoring flights were missed due to inclement weather. However, even with inexact dates, researchers conducting the VHF-based studies detected a chronological order for entering and exiting dens that was similar to our findings decades later (Russell *et al.* 1979*; Horejsi and Raine 1983*). GPS collars allowed us to determine precise denning dates and should allow researchers to identify changes in denning duration that may be important for detecting impacts of climate change on Grizzly Bear den biology in the future.

Conservation implications

GPS collars allowed biologists to collect large datasets on movements of individual bears, to determine accurate estimates for home range, and to determine hourly movement rates and precise denning dates. These data permit biologists to compare the biology of the Grizzly Bear across its range and test hypotheses not possible with VHF data. Although VHF-based studies provided home range estimates, they could under-

estimate the true area and movement data were limited. Denning chronology by age–sex–reproductive class was recognized in VHF-based studies, but precise dates were lacking. VHF-based studies required biologists to locate their animals visually, which often involving dangerous low-level flying, but offered opportunities for direct observations. GPS collars provide accurate and abundant data, but ethological observations are often minimal. Observations of individual animals and site visits to GPS locations are crucial for interpreting GPS telemetry data and should be an important component of any research project that employs GPS collars on wildlife.

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