

## Quantifying spatial–temporal patterns in wildlife ranges using STAMP: A grizzly bear example

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### A B S T R A C T

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Geographical spatial analysis approaches are ideally applied to studies of wildlife habitat use when spatial data, such as telemetry data or spatial ranges, are available. For instance, it is often desirable to quantify spatial–temporal patterns of home ranges, which are typically delineated as polygons and represent areas of habitat that support wildlife functions. Changes to home ranges over time are often presented as variation in mean polygon area. This two-dimensional approach ignores potentially important spatial–temporal characteristics of habitat use, including site fidelity, range contraction, and expansion. Using Spatial–Temporal Analysis of Moving Polygons (STAMP) we examined a set of movement data for a subpopulation of adult female grizzly bears (*Ursus arctos*) for the period from 1999 to 2003 in the Rocky Mountain foothills region of Alberta, Canada. Home range change was quantified over two-year periods and evaluated on the basis of variable offspring dependency (i.e., whether the females had no cubs, cubs-of-the-year (COY), or yearling cubs) and foraging season. Solitary bears showed the greatest amount of home range fidelity, with an increase in range size during the mating season. Female grizzly bears with offspring experienced substantial home range change. Sows with COY had a reduced maternal home range size, especially during mating season, while those with yearling offspring had an increased home range size. The patterns of home range change were consistent with those expected if some combination of mobility and infanticide were the driving ecological mechanisms. We conclude that offspring dependency does not impact the degree of site fidelity but does impact the nature of home range change experienced. We also suggest that the spatial–temporal change in female grizzly home ranges could be used to infer breeding status and as a population monitoring tool. A geographical approach to home range change provides a simple and quantitative approach to mapping spatial–temporal patterns of habitat use and animal movement.

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### Introduction

Understanding the relationship between wildlife movements and habitat use is a cornerstone for management of wildlife populations. Accordingly, radiotelemetry has been widely used as it provides accurate depictions of the activities and area used by animals (e.g., Amstrup & Beecham, 1976; Cochran & Lord, 1963). An animal's home range is typically depicted as a polygon constructed around a set of animal location points. Home ranges are often used to explore the relationship between wildlife behaviour and

environmental space use (Borger et al., 2006; Morales, Fortin, Frair, & Merrill, 2005; Schwab & Zandbergen, 2011).

While it is useful to know mean home range area (Carfagno & Weatherhead, 2008; Laver & Kelly, 2008), standard metrics lack detail on spatial location and structure of the home range. In other words, while the size of a given home range may not change over time, its geometric configuration and spatial location may, in fact, shift to the extent that a given animal is using substantially different habitat. This issue becomes particularly problematic for low-density wide-ranging populations in highly heterogeneous landscapes (Apps, McLellan, Woods, & Proctor, 2004; Wielgus & Bunnell, 1995) or when there is high inter-population variability in behaviour (e.g., Wiens, Crawford, & Gosz, 1985).

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The notion of shifting home ranges relates to the concept of home range fidelity, which has been described for a number of vertebrate species (Borger et al., 2006; Freedman & Roy, 2012; Switzer, 1997). Home range fidelity occurs when a particular animal leaves a given site, say upon migration or hibernation, but returns to the previously occupied and familiar site (Switzer, 1993). The benefit accrued with familiarity of a habitat (including resources and competition) is weighed against the costs of the animal making its way back to this habitat (Edwards, Nagy, & Derocher, 2009). In contrast, when there is low spatial–temporal predictability of resources within a given home range, resource acquisition may be maximized by venturing into neighbouring areas (Maher & Lott, 1995; Wiens, 1976). This results in a shift to the home range, which is sometimes referred to as home range infidelity or drift (Doncaster & MacDonald, 1991; Edwards et al., 2009). Unfortunately, there is a dearth of information on home range fidelity and drift in both space and time (Borger et al., 2006; Switzer, 1997), likely due to a lack of analytical methods for capturing and characterizing dynamic processes of space use.

Living under mounting anthropogenic pressures, the threatened grizzly bears in the Rocky Mountain eastern slopes region of Alberta, Canada are faced with the region's increasing economic growth and development, mainly from natural resource extraction. Considering that economic growth has been cited as a limiting factor for wildlife conservation (Czech & Daly, 2004; Czech & Krausman, 1997), grizzly bears in this region have been the subject of numerous studies to better understand their habitat use and requirements (e.g., Mace, Waller, Manley, Ake, & Wittinger, 1999; Mace, Waller, Manley, Lyon, & Zuuring, 1996; Munro, Nielsen, Price, Stenhouse, & Boyce, 2006; Nielsen, Boyce, & Stenhouse, 2004; Stenhouse et al., 2005). Bear habitat in the eastern slopes has been found to be highly fragmented from natural resource activities including mining, oil and gas exploration and forest harvesting (Linke, Franklin, Huettmann, & Stenhouse, 2005; Nielsen et al., 2004). Here, grizzly bears occur at relatively low population densities (e.g., 4.79 bears per 1000 km<sup>2</sup>) (Boulanger et al., 2005). The foraging behaviour, and thus habitat requirements, of these bears can be temporally partitioned into three distinct seasons: spring (hypophagia), summer (early hyperphagia), and autumn (late hyperphagia) (Nielsen, Boyce, Stenhouse, & Munro, 2003, 2004).

Female grizzly bears provide exclusive parental care (Clutton-Brock, 1991), and previous studies of grizzly bear home ranges have described general patterns of sex–age habitat segregation related to the movement constraints imposed by offspring of varying dependence (Dahle & Swenson, 2003a; Wielgus & Bunnell, 1995). Specifically, maternal home ranges have been shown to be smaller than those of solitary adult female grizzlies, with the home ranges of females with cub-of-the-year (COY) the smallest (Blanchard & Knight, 1991; Dahle & Swenson, 2003a, 2003b).

In this study we demonstrate how a geographic method that quantifies change in polygons over time, Spatial–Temporal Analysis of Moving Polygons (STAMP) (Nelson, 2011; Robertson, Nelson, Boots, & Wulder, 2007), may be used to characterize the seasonal home range fidelity of female grizzly bears and quantify the variable impact of offspring. We hypothesize that solitary bears will exhibit the most home range fidelity (Dahle & Swenson, 2003a). Further, we hypothesize that bears with offspring will demonstrate greater amounts of home range change, especially females with COY (Blanchard & Knight, 1991; Dahle & Swenson, 2003a).

## Methods

### Study area

We conducted our study along the eastern slopes of the Canadian Rocky Mountains in west-central Alberta (53°25'N, 117°34'W,

Fig. 1) over a 38,705 km<sup>2</sup> area. The average temperature ranges from 11.5 °C in the summer to –6.0 °C in the winter and the annual precipitation is 538 mm (Beckingham, Corns, & Archibald, 1996). The local climate is strongly influenced by the elevation, which varies from 770 m to >3500 m.

The study area is characterized by a gradient of human intensity and development, with protected areas dominating the mountains in the west and resource extraction in the rolling foothills in the east. The mountainous land cover consists of montane forests, conifer forests, sub-alpine forests, alpine meadows, and high elevation rock, snow, and ice (Achuff, 1994; Franklin et al., 2001). Approximately one-third of the area is protected, predominately in the high elevation mountain area, which includes Jasper National Park (10,179 km<sup>2</sup>), Willmore Wilderness Park (1791 km<sup>2</sup>), and Rock Lake-Solomon Creek Wildland Provincial Park (330 km<sup>2</sup>). These mountainous areas are characterized by extensive recreational use. In contrast, the eastern foothills region is characterized by forestry; mining; oil and gas exploration and development; trapping, hunting, and other recreation (Linke et al., 2005; Nielsen et al., 2004; Nielsen, Stenhouse, & Boyce, 2006; Stenhouse et al., 2005). An extensive road and seismic line network, the result of resource extraction activities, intersects the study area. Large-scale timber harvesting, which began in mid 1950s, has resulted in increased fire suppression (Andison, 1998; Nielsen et al., 2004). The land cover in the foothills region consists of forests (conifer, mixed, deciduous, and regeneration), open treed-bogs, and small herbaceous meadows (Stenhouse et al., 2005).

### Grizzly bear telemetry data and home range delineation

As part of the Foothills Research Institute Grizzly Bear Program, telemetry data was collected for 61 grizzly bears from 1999 to 2003 (Cattet, Christison, Caulkett, & Stenhouse, 2003). Bears were captured and collared using aerial darting and leg-hold snaring (Stenhouse & Munro, 2000). All capture efforts followed protocols accepted by the Canadian Council of Animal Care for the safe handling of bears (Animal Use Protocol number 20010016). Each captured grizzly bear was fitted with either a Televilt (Lindesberg, Sweden) Simplex GPS radio collar or an Advanced Telemetry System (ATS, Isanti, Minnesota, USA) GPS radio collar. Both types of collars logged a spatial location at minimum every 4 h, with a positional accuracy of approximately 10–20 m (Linke et al., 2005; Stenhouse & Munro, 2000).

Following previous grizzly bear research (e.g., Munro et al., 2006; Nielsen et al., 2004; Stenhouse et al., 2005; Stewart, Nelson, Wulder, Nielsen, & Stenhouse, 2012), we partitioned the telemetry data based on the seasonal shifts in food habitats and resource selection patterns into spring (1 May to 15 June), summer (16 June–15 August), and autumn (16 August–15 October) (Nielsen et al., 2003, 2004).

We examined the seasonal home range of grizzly bears for a minimum of two consecutive years, time period 1 ( $T_1$ ) and time period 2 ( $T_2$ ), between 1999 and 2003. The home ranges were partitioned by the age of dependent offspring as follows: (1) solitary adult females in both  $T_1$  and  $T_2$ ; (2) solitary in  $T_1$  and COY present in  $T_2$ ; and (3) COY in  $T_1$  and yearling present in  $T_2$ . Included in the second category, solitary in  $T_1$  and COY in  $T_2$ , were the two instances where a mother lost her yearling in  $T_1$  but had a COY in  $T_2$ . With bears that were monitored for three or more consecutive years, we compared their solitary home ranges ( $T_1$ ) to their dependent yearling home ranges ( $T_2$ ). This offspring category examines the range size and range location before and after having a COY.

We selected bears with  $\geq 50$  telemetry locations per season for a minimum of two consecutive years and restricted consecutive

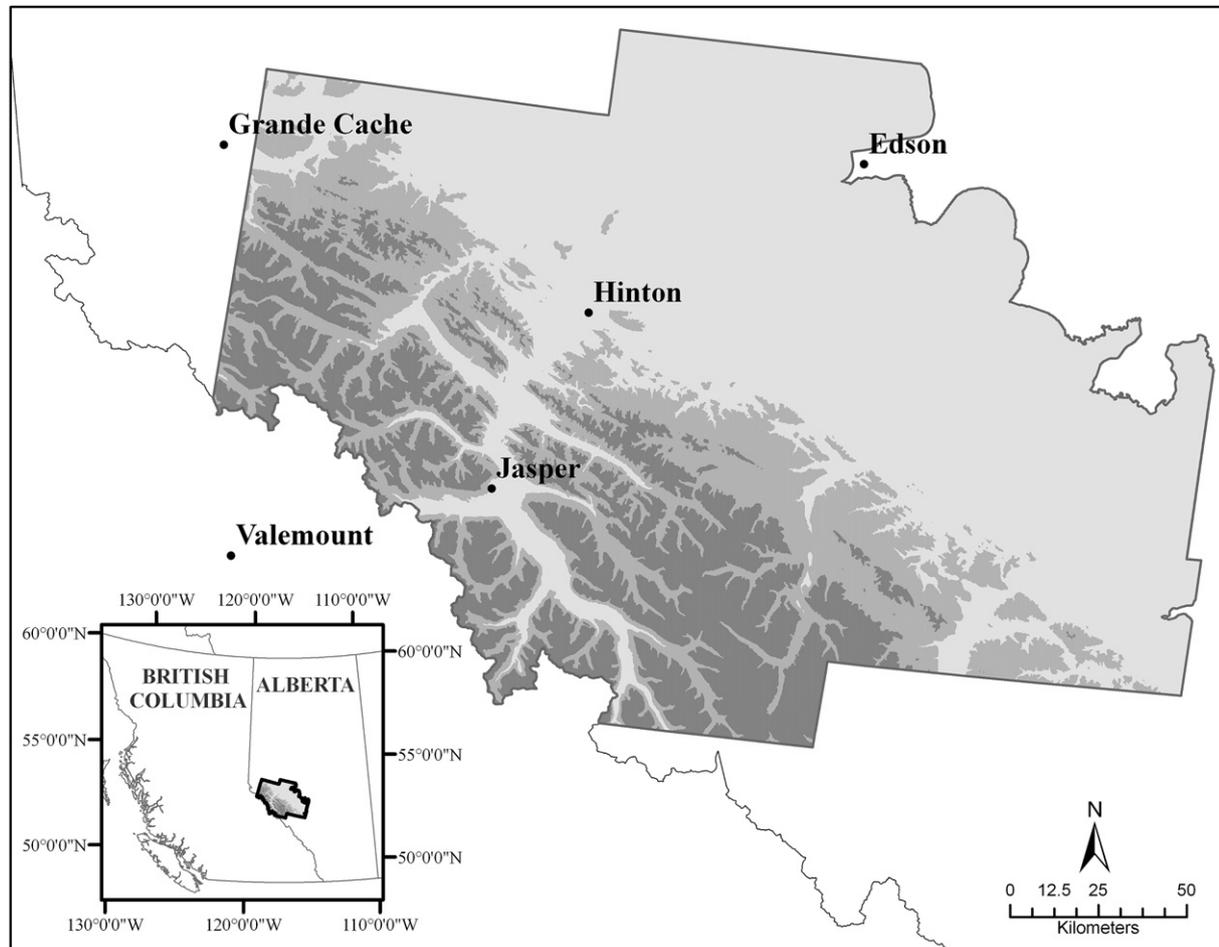


Fig. 1. Surrounding towns and elevation within the study area. Study area location within Alberta is depicted in the lower left portion of the figure.

year seasonal home ranges to those that had a similar number of telemetry points in both years, resulting in the analysis of 11 different female bears. When the bears were further partitioned by season, 37 pairs of consecutive-year bear location data were used in this study.

We delineated home ranges using kernel density estimation (see [Worton, 1987](#) for details), which is the most common method for characterizing and modelling home ranges ([Borger et al., 2006](#); [Mace et al., 1996](#); [Seaman & Powell, 1996](#)), including grizzly bear home ranges (e.g., [Mace et al., 1996](#); [Mace & Waller, 1997](#)). Following previous studies, we used the 95% isopleth of the kernel density to define home range boundaries (e.g., [Garshelis, Gibeau, & Herrero, 2005](#); [Mace et al., 1996](#)).

#### Quantifying change in size and pattern of home ranges

We quantified the relative and absolute change in seasonal home range size between  $T_1$  and  $T_2$  for each offspring dependency. To determine if the home range area in  $T_1$  and  $T_2$  were significantly different, we computed a Paired Student's *T*-test, which can be applied for small sample sizes of data in consecutive years. The test was calculated for offspring dependencies using at least 5 bears.

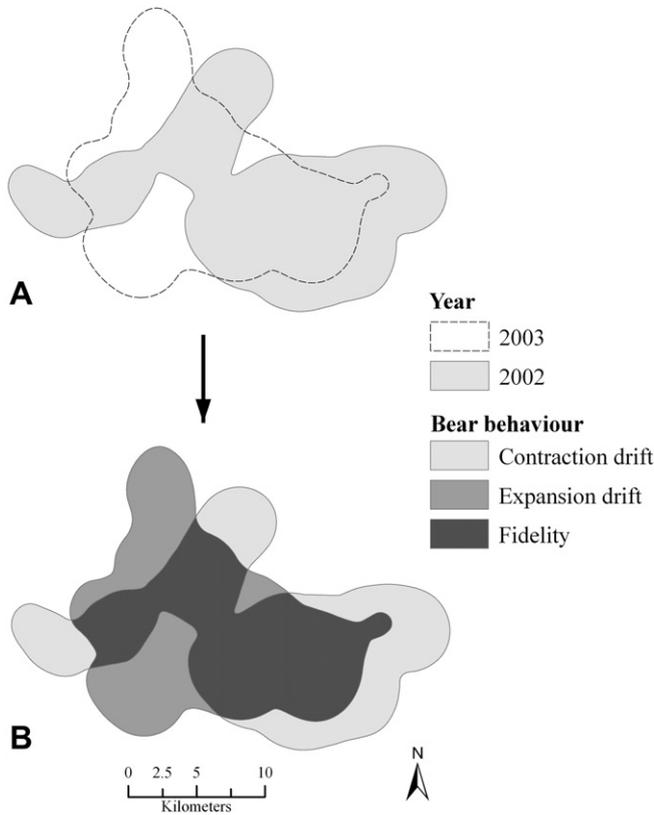
Following [Nelson \(2011\)](#), we employed STAMP for quantifying home range change (HRC). Change in spatial–temporal pattern was defined as the union of two annual home range polygons for an individual bear in  $T_1$  and  $T_2$ . The HRC is composed of STAMP events (i.e., new polygons generated through the union of two home

ranges) that describe the spatial relationship that occurred between  $T_1$  and  $T_2$  ([Fig. 2](#)). Three specific STAMP events were defined: stable (fidelity), contraction (drift), and expansion (drift). A stable event, hereafter known as fidelity, occurs when habitat is used consistently in both  $T_1$  and  $T_2$  and indicates that habitat areas were used repetitively. An expansion event occurs when new habitat is used in  $T_2$  that was not used in  $T_1$  and indicates areas of home range *growth*. A contraction event occurs when habitat is used in  $T_1$ , but is no longer used in  $T_2$ , and indicates areas home range *loss*. To facilitate comparisons of STAMP patterns with changes in home range size, we calculated the absolute area and the relative proportion of each STAMP event (fidelity, contraction, and expansion) by dividing the area of the event by the total HRC area. To assess whether the area of fidelity, contraction, and expansion were significantly different we calculated a Paired Student's *T*-test. The test was calculated for offspring dependencies using a minimum of 5 bears.

## Results

#### Home range delineation and size

Yearly seasonal home ranges were estimated from 10,580 location data collected on adult female grizzly bears between 1999 and 2003. A total of 51 home ranges were delineated from an average of 212 ( $n = 51$ ,  $\sigma = 73$ ) locations. The average home range size varied depending on offspring dependency and season



**Fig. 2.** Example STAMP input and results for a bear in autumn from 2002 to 3. The input polygons (A) are the autumn home ranges for a bear in 2002 and 2003. The STAMP results (B) is the home range change (HRC) for the bear; the bear behaviour identified are contraction drift, expansion drift, and fidelity.

(Table 1), with bears with COY having the smallest average home range (200 km<sup>2</sup>,  $n = 19$ ,  $\sigma = 110$  km<sup>2</sup>).

**Change in home range size**

When change in home range size was examined, we observed a decrease in home range size of 21% for bears remaining solitary, while had COY in T<sub>2</sub> decreased by 40% ( $T = 3.57$ ,  $P = 0.0015$ ) (Table 2). The home range size of bears with a yearling in T<sub>2</sub> increased by 85% ( $T = -1.91$ ,  $P = 0.068$ ). Home ranges averaged 20% larger for females with yearling offspring compared to their ranges

**Table 1**  
Home range<sup>a</sup> size (km<sup>2</sup>) categorized by offspring dependency and season for adult female grizzly bears.

Female offspring dependency	Foraging season	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	$n$
Solitary	spring	435	198	5
	summer	366	87	7
	autumn	278	174	7
COY <sup>b</sup>	average	352	160	
	spring	147	83	4
	summer	205	139	8
Yearling	autumn	226	86	7
	average	200	110	
	spring	404	314	5
	summer	354	194	5
	autumn	267	27	3
	average	332	182	

<sup>a</sup> home range defined as the 95% contour of the kernel density estimation.  
<sup>b</sup> Cub-of-the-year.

**Table 2**  
Seasonal change in home range size categorized by offspring dependency for adult female grizzly bears.

Female bear offspring dependency		Change area			$n$
T <sub>1</sub>	T <sub>2</sub>	$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	
Solitary	Solitary	-21	-129	176	3
Solitary	COY <sup>a</sup>	-40	-181	170	13
COY <sup>a</sup>	Yearling	85	117	145	13
Solitary	Yearling	20	-52	160	8

<sup>a</sup> Cub-of-the-year.

while solitary (2 years prior) ( $T = 0.484$ ,  $P = 0.64$ ). Bears with a single dependent offspring experienced an average home range area change of 41% ( $n = 6$ ,  $\sigma = 28\%$ ), whereas bears with 2 dependent offspring experienced a 72% change ( $n = 14$ ,  $\sigma = 64\%$ ), and bears with 3 dependent offspring experienced an 80% change ( $n = 6$ ,  $\sigma = 137\%$ ) in area. These changes, however, were not significant.

Changes in home range size were partitioned by grizzly bear foraging season (Table 3). Bears remaining solitary had the greatest change in relative home range area in autumn (-59%). For bears with offspring, the most substantial changes in relative home range area occurred in spring, when bears with dependent COY had a 70% decrease in home range size and bears with dependent yearling offspring increased their home range size 135% from the previous year. To a lesser extent, the remaining two seasons continued to show a decrease in area for bears with COY in T<sub>2</sub> (54% in summer, and 7% in autumn) and increase for those with yearlings in T<sub>2</sub> (95% in summer, and 44% in autumn).

**Home range pattern**

Using STAMP to quantify the spatial relationship between all home ranges in T<sub>1</sub> and T<sub>2</sub>, we found the average area of home range fidelity was 41% ( $n = 37$ ,  $\sigma = 18\%$ , range 15–82%), while the area of contraction was 32% ( $n = 37$ ,  $\sigma = 28\%$ , range 0–82%) and expansion was 27% ( $n = 37$ ,  $\sigma = 21\%$ , range 0–79%). When categorized by offspring dependency (Table 4), the home range of bears remaining solitary experienced the largest proportion of home range fidelity (54% of the area). The home range of bears solitary in T<sub>1</sub> and with COY in T<sub>2</sub> had substantial amounts of contraction (52% of the area) and smaller amounts of fidelity (35% of the area). The area of contraction, expansion, and home range fidelity were different

**Table 3**  
Change in home range size categorized by offspring dependency and season for adult female grizzly bears.

Female bear offspring dependency		Foraging season	Change in home range area			$n$
T <sub>1</sub>	T <sub>2</sub>		$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	
Solitary	Solitary	spring	-10	-29	0	1
		summer	7	19	0	1
		autumn	-59	-376	0	1
Solitary	COY <sup>a</sup>	spring	-70	-390	111	3
		summer	-54	-219	106	5
		autumn	-7	-18	49	5
COY <sup>a</sup>	Yearling	spring	135	246	183	3
		summer	95	121	118	5
		autumn	44	186	37	5
Solitary	Yearling	spring	-20	-132	149	2
		summer	-25	-65	78	2
		autumn	43	-6	178	4

<sup>a</sup> Cub-of-the-year.

**Table 4**  
Area of range expansion, contraction and site fidelity categorized by offspring dependency for adult female grizzly bears.

Female bear offspring dependency		Area of site fidelity and range drift									n
T <sub>1</sub>	T <sub>2</sub>	Contraction			Expansion			Fidelity			
		$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	
Solitary	Solitary	-32	191	199	14	63	23	54	208	46	3
Solitary	COY <sup>a</sup>	-52	239	164	13	67	41	35	127	42	13
COY <sup>a</sup>	Yearling	-14	70	58	42	177	151	44	155	79	13
Solitary	Yearling	-40	123	68	28	175	123	32	221	151	8

<sup>a</sup> Cub-of-the-year.

( $P < 0.05$ ) for the solitary to COY offspring dependency. COY to yearling changes in maternal home range had nearly equal amounts of expansion (42% of the area) and fidelity (44% of the area) ( $T = 0.451$ ,  $P = 0.66$ ). The area of contraction, however, was different from expansion ( $T = 2.11$ ,  $P = 0.046$ ) and fidelity ( $T = -3.35$ ,  $P = 0.0026$ ). The area of expansion ( $T = -2.76$ ,  $P = 0.011$ ) and contraction ( $T = -3.58$ ,  $P = 0.0015$ ) differed between bears that were solitary in T<sub>1</sub> but had a COY in T<sub>2</sub> compared to those that had a COY in T<sub>1</sub> but had a yearling in T<sub>2</sub>. The ranges of bears with yearling offspring experienced notable contraction (40%) compared to the ranges of solitary bears, despite there being no significant differences in the amount of expansion or fidelity.

We compared the amount of fidelity between seasons, regardless of offspring dependency, and found no statistically significant differences. When a bear had a COY in T<sub>2</sub>, it experienced substantial amounts of contraction in spring (73%) compared to the previous solitary year (Table 5). The proportion of contraction decreased in summer (57%) and was the smallest in autumn (33%). When a bear had a yearling in T<sub>2</sub>, expansion accounted for 56% of the change in area in spring, 38% in summer, and 35% in autumn. The home ranges of solitary bears compared to their with-yearling home ranges exhibited predominantly home range fidelity, with the exception of autumn when their home range experienced greater amounts of contraction (43%).

## Discussion

The observed spatial–temporal pattern in grizzly bear home ranges is similar to that predicted by the maternal care and state-dependent mobility hypotheses of Dahle and Swenson (2003b) that examined the reproductive strategies of female bears. We found that the relationship between home range size, fidelity, and drift (expansion and contraction) changed along a gradient of

offspring dependency. Our results also support the notion that season impacts home range size and fidelity changes, whereby the greatest change occurs in spring for bears with COY and yearlings (Blanchard & Knight, 1991; Dahle & Swenson, 2003b). Similar patterns of young offspring impacting the maternal range have been noted in other species, including sea lions (*Zalophus wollebaeki*) (Wolf & Trillmich, 2007), leopards (*Panthera pardus*) (Odden & Wegge, 2005; Seidensticker, 1976), tigers (*Panthera tigris*) (Sunquist, 1981), Iberian lynx (*Lynx pardinus*) (Fernandez & Palomares, 2000), and mountain lions (*Felis concolor*) (Hemker, Lindzey, & Ackerman, 1984).

A possible mechanism for maternal home range change, unrelated to offspring status, is resource availability (McLoughlin & Ferguson, 2000; Myer, McCown, & Oli, 2007). Home range size should decrease when food abundance increases because individuals are able to obtain sufficient resources in a smaller area (Boutin, 1990; Said et al., 2005). This trend has been observed in black bears (Powell, Zimmerman, & Seaman, 1997) and grizzly bears (Craighead, Sumner, & Mitchell, 1995). Changes in resource availability should be especially pronounced in the home ranges of solitary females since they are primarily concerned with foraging, not with rearing young. Over our five year study, we found that all home range size changes operated similarly regardless of the year even though two years (2001 and 2002) had about a third less precipitation than the 30-year normal.

Changes in home range size could be due to the individual behavioural characteristics of the bears. For example, research on small mammals has shown that home range size is a function of dispersal distance in which individuals with larger home ranges often had greater dispersal distances (Bowman, Jaeger, & Fahrig, 2002). However, if this was the case for adult female bears in our study, individual bears with larger home ranges would experience large amounts of contraction and expansion while maintaining

**Table 5**  
Area of range contraction, expansion, and fidelity categorized by offspring dependency and season for adult female grizzly bears.

Female bear offspring dependency		Foraging season	Area of site fidelity, contraction and expansion									n
T <sub>1</sub>	T <sub>2</sub>		Contraction			Expansion			Fidelity			
			$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	$\bar{x}$ (%)	$\bar{x}$ (km <sup>2</sup> )	$\sigma$ (km <sup>2</sup> )	
Solitary	Solitary	spring	-26	84	0	17	56	0	57	184	0	1
		summer	-6	19	0	12	39	0	82	271	0	1
		autumn	-64	470	0	13	94	0	23	167	0	1
Solitary	COY <sup>a</sup>	spring	-73	456	129	5	37	48	22	130	35	3
		summer	-57	246	96	7	27	30	36	146	45	5
		autumn	-33	103	59	25	85	49	42	106	35	5
COY <sup>a</sup>	Yearling	spring	-13	46	42	56	292	214	31	113	42	3
		summer	-9	52	84	38	173	127	53	182	88	5
		autumn	-20	76	45	35	113	61	45	154	73	5
Yearling	Solitary	spring	-16	136	58	34	268	91	51	421	117	2
		summer	-11	50	43	36	115	35	53	211	92	2
		autumn	-43	152	55	30	159	139	28	127	74	4

<sup>a</sup> Cub-of-the-year.

a relatively consistent home range size. Contrary to the dispersal distance hypothesis, individual bears in our study experienced contraction and expansion relative to their offspring status.

There are several possible explanations for the observed offspring-related changes in home range size. First, the metabolic, or energetic hypothesis, states that home range size of mammals should increase with increasing body mass (McNab, 1963). Dahle and Swenson (2003a) predicted that the metabolic needs of females with young should exceed those of lone females, as offspring are provided with milk and the total body mass of a family group could be twice that of a lone female. As a result, females with yearling offspring and/or greater number of dependants should have the largest home range, as they have the largest total body mass. Contrary to the metabolic hypothesis, and in agreement with Dahle & Swenson's (2003a) findings, ranges of solitary females were significantly larger than females with COY, but were not significantly different from females with yearlings. Our comparisons of females with multiple offspring were inconclusive due to small sample sizes. However, McLoughlin and Ferguson (2000) also found that body mass related factors were not the most important determinants of grizzly bear home range size.

An additional possible explanation for the changes in home range size that we observed is the limited mobility of young dependent offspring. In spring and early summer, COY are small and this may limit the movements of the mother (see Blanchard & Knight, 1991; Dahle & Swenson, 2003b; Hirsch, Bender, & Haufler, 1999; Lindzey & Meslow, 1977). Alternatively, but resulting in the same outcome, females may restrict movement as the ability for young cubs to evade predation is more limited than with older cubs. Predation risk may also increase in unfamiliar areas since bears may need more time to hide or find escape routes than in familiar locations, as has been found in other species (Janmaat, Olupot, Chancellor, Arlet, & Waser, 2009). Intraspecific infanticide is known to be a significant cause of grizzly cub mortality (Blanchard & Knight, 1991; Dahle & Swenson, 2003b; Powell et al., 1997; Rode, Farley, & Robbins, 2006; Wielgus & Bunnell, 1995). Male bears are known to travel widely in search of breeding opportunities (Dahle & Swenson, 2003a; Sandell, 1989; Swenson, Dahle, & Sandegren, 2001), and it is during this time (i.e., late May to early July) that the risk of infanticide is greatest (Bellemain, Swenson, & Taberlet, 2006; Dahle & Swenson, 2003b). The home range size for bears with COY in autumn (post-mating season) increased, possibly as the seasonal threat of infanticide was alleviated, as also noted by Swenson et al. (2001). However, confounding these ideas is the fact that by autumn offspring are reaching yearling size and would have increased mobility and also be less vulnerable to predation risk by other species.

The solitary females in our study had the largest home ranges in spring. The increase in home range size in spring may result from the wide distribution of food resources during this season, causing the bear to travel great distances to find food (Munro et al., 2006). Spring is also mating season. The increase in home range size during mating season may be especially important in low density populations to increase a solitary female's chances of mating with multiple partners (Bellemain et al., 2006). This promiscuous behaviour has been suggested to enhance paternal uncertainty and reduce the possibility of infanticidal behaviour (Bellemain et al., 2006; Ebensperger, 1998; Hrdy, 1979).

The changes in the spatial pattern of fidelity, contraction and expansion correspond with observed dynamic shifts in home range size. Female bears in our study area exhibited greater fidelity (41%) than bears observed by Edwards et al. (2009) in the Canadian Arctic (24%, range 6–37%). This interpretation is confounded, however, as their study also included male bears, which are known to exhibit less fidelity to seasonal and annual home ranges than females

(Blanchard & Knight, 1991). Similar to the results of Blanchard and Knight (1991), we found no significant differences in the amount of home range fidelity between offspring classes, potentially indicating that a core home range area may be used repeatedly regardless of offspring class. Ranges for solitary females remained the most spatially consistent between years.

The amount of home range fidelity may change seasonally, but the small sample sizes ( $n \leq 5$ ) limit our scope of inference. Nonetheless, it appears that bears in this study are most faithful to their seasonal home ranges in summer. Blanchard and Knight (1991) reported that female grizzlies in the Yellowstone region had the greatest home range fidelity to their spring ranges, followed by autumn, and then summer ranges. Although our boreal forest study area is quite different than the subarctic, Edwards et al. (2009) reported no significant differences in seasonal home range fidelity for a population of grizzly bears in the western subarctic of Canada.

With regards to range contraction and expansion, we found differences depending on offspring dependency; bears with COY experienced significantly more contraction and less expansion than bears with yearlings. The pattern of home range change varied seasonally with the greatest magnitude of contraction and expansion occurring in spring, then summer, and to the least extent, autumn. The spatial pattern of fidelity, expansion, and contraction show the dynamic space use of grizzly bears over time and in relation to offspring.

Our study focuses on grizzly bear movement in relation to offspring status. Animal movements, however, are the result of complex interactions between an individual animal and its external environment (Forester et al., 2007). Other potential reasons for movement that undoubtedly contributed to the movement of the bears in this study and have not been accounted for include noise, stress, disturbance, habitat fragmentation and social interactions.

Depending on the scale and depth of future studies quantifying home range change, it might be useful to examine the telemetry data further to determine changes in areas of intense use, or core areas, within the home range. Core areas may be identified using utilization distributions which show of the relative frequency distribution of an animal's locations over a specified period of time (Van Winkle, 1975). Nelson (2011) examined changes in core areas by comparing the wildlife utilization distribution (in the form of KDE surfaces) from two time periods. As a result, changes in pockets of home range use were identified.

Based on the individual spatial-temporal home range changes observed in this study, we suggest that there is the potential to apply the behavioural changes quantified by STAMP to infer the breeding status of adult female bears. Typically studies, including this, assess the offspring status of mammals through ground or aerial observations. A few studies, however, have shown the use of radiotelemetry to estimate breeding status (e.g., Bradley, Cooke, Loughheed, & Boyd, 2004; Green, Tyler, Stowe, & Newton, 1997). Specifically, based on the movement patterns of individuals, Bradley et al. (2004) was able to determine the breeding status and success of marbled murrelets (*Brachyramphus marmoratus*). For secretive species that are sensitive to human disturbance, estimating offspring dependency from telemetry data, as opposed to direct observation, would be a valuable population monitoring tool for management. With the application of STAMP, managers may be able to hypothesize if an individual bear's offspring status has changed based on the behavioural changes quantified by the spatial patterns of home range fidelity and drift. For example, if a bear's home range contracts in area by 40–50% and these changes are most pronounced in spring, managers may predict that the bear has had a COY. It would be beneficial to test the abilities of STAMP on predicting offspring status in future studies of bears both in this population and in other study areas.

The calculation of animal home range is an example of an ecological model that predicts habitat use based on a sample of data. We use a GIS method (i.e., STAMP) for modelling changes in polygon structures to demonstrate how offspring influences the spatial ranges of female grizzly bears. Prediction models use algorithms to establish a relationship between inputs (e.g., telemetry data and offspring status) and responses (e.g., bear movement) and to find dominant patterns (Elith, Leathwick, & Hastie, 2008). The core of predictive modelling in ecology has been the quantification of species–environment relationships (Guisan & Zimmermann, 2000). In contrast, fitting statistical models involves selecting the correct statistical model and determining parameters for this model from the data (Elith et al., 2008). Model fitting hinges on the correct selection of parameters and parsimony. The strength of spatial pattern approaches, such as we have taken here, are the ability to quantify relationships that impact spatial distributions and to highlight parameters appropriate for future model parameterization.

## Conclusion

Using a geographical and spatially explicit method for examining the dynamics of home range changes, STAMP, we were able to examine dynamics of habitat use and space–time patterns of animal movement in relation to the ecological concepts of home range fidelity and drift. Geographical methods are increasingly being utilized in ecology and biogeography (Nelson & Boots, 2008) and enable the spatial–temporal variability in spatially explicit telemetry data sets to be quantified (e.g., Fortin, Dale, & Bertazzon, 2010; Long & Nelson, 2012; Nelson, 2011). In this manuscript we have applied the simplest functionality of STAMP and have demonstrated its utility for quantifying space–time pattern of female grizzly bear habitat use. There are several methodological extensions that can be applied to STAMP (e.g., Nelson, 2011). The mappable output of STAMP can be integrated within a GIS framework and environmental covariate utilized to further analysis. As well, STAMP has directional functionality (Robertson et al., 2007) that can be employed when hypotheses on wildlife direction, such as range expansion based on climate change, are of interest.

We demonstrate that solitary bears exhibit the most fidelity to their home ranges, relative to female bears with offspring. In addition, home range change was found to be greater for females with offspring than those remaining solitary. We further conclude that offspring dependency impacts the nature and quantity of home range change (i.e., expansion or contraction). This current examination of the effect of offspring dependency adds to the growing research on home range fidelity, which has included studies on the impact of age (Janmaat et al., 2009; Schaefer, Bergman, & Luttich, 2000), reproductive success (Switzer, 1997), parental territories (Murray, Gilby, Mane, & Pusey, 2008), study scale (Janmaat et al., 2009), and resource distribution (Edwards et al., 2009).

We have also proposed the use of STAMP to estimate offspring dependency from telemetry data. We feel that further studies are required, but we believe that STAMP has utility for other species whose movement patterns might be used to assess offspring status. The ability to remotely assess offspring status for secretive species by movement pattern analysis would be a valuable population monitoring tool for management and conservation biology.

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